Paleoindicators

of

Meromixis

by

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Well, one must learn

By doing the thing; for though you think you know it,

You have no certainty until you try.

Sophocles

ABSTRACT

This study was undertaken to ascertain whether meromictic lakes could be differentiated from holomictic lakes on the basis of their surficial profundal sediments. Surface sediment cores (15 cm long) were collected from both the littoral and profundal zones of four meromictic and six holomictic lakes and analyzed for total number of fossil chironomid headcapsules, chlorophyll and carotenoid degradation products as well as iron and manganese concentrations.

Littoral and profundal comparisons of the surface sediments were made between the two lake types using the Mann-Whitney U test. Iron, manganese and the iron to manganese ratio in the littoral sediments of meromictic lakes were significantly lower than those found in the littoral sediments of holomictic lakes. The observed differences are believed to represent an artifact of the significantly higher carbonate concentrations found in three of the four meromictic lakes studied.

Profundal and littoral to profundal ratio comparison between holomictic and meromictic lakes suggest that the significantly lower iron and higher carotenoid concentrations in meromictic profundal sediments were a consequence of meromixis. However, the overlap in distribution exhibited by both iron and carotenoid degradation products between the two lake types was sufficiently large in this study to nullify their use as a means of differentiating meromictic from holomictic lakes.

A long core (4.25 m) was removed from the deepest part of the meromictic Crawford Lake (Ontario), sectioned at 5 cm intervals, and

analyzed to assess when meromixis occurred, based on its fossil record. Temporal changes in the total number of chironomid headcapsules, and chlorophyll and carotenoid sediment degradation products were closely correlated with organic matter, indicating in my opinion that extensive redeposition of littoral chironomid headcapsules in the profundal zone has occurred. Temporal variations in carotenoid degradation products, in response to changes in organic matter, obscured increased preservation that may have occurred as a consequence of meromixis. Temporal variations in iron and manganese suggest that relatively stable redox conditions have existed throughout most of the lake's history. Therefore it would appear that Crawford Lake has been meromictic since its inception.

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I. INTRODUCTION

Glacial lakes in north temperate regions of the world were formed during the Pleistocene Epoch, roughly 10,000 to 12,000 years ago. At present, two basic lake types are recognized (meromictic and homomictic), based on their vertical circulation patterns. A third type (oligomictic) was suggested by Hutchinson and Loffler (1956), however, the term is ambiguous as there is no clear-cut distinction between oligomictic lakes, and meromictic or holomictic lakes (Walker and Likens, 1975).

Meromictic lakes differ from holomictic lakes in that only partial circulation of the water column occurs in the former. The bottom non-circulating layer of water, termed the monimolimnion, remains anaerobic for extended periods of time. Meromixis, however, is not necessarily a permanent state. Halls lake, Washington, was meromictic for approximately fifty years (1915-1963), circulated completely in 1963 and has been essentially holomictic ever since (Culver, 1973).

This study was undertaken to determine whether the biological and chemical differences existing between surface holomictic and meromictic lacustrine sediments can be applied to paleolimnological studies, indicating if and when meromixis was first initiated in lake development. Three variables based on lake sediment examination were used to determine such differences and to detect past periods of meromixis. The three factors selected were: (1) the total number of fossil chironomid head capsules present, (2) the iron to manganese ratio, and (3) the preservation of plant pigments. The rationale for using each variable is described in the following review.

A. FOSSIL CHIRONOMID HEADCAPSULES

The headcapsules of chironomid larvae are composed of chitin which is relatively inert chemically (Frey 1976), and thus are generally well preserved in lake sediments. During the development of several meromictic lakes, temporal changes in the total number of fossil chironomid headcapsules have been suggested as indicators of meromixis initiation (Frey 1955, Dickman *et al.* 1974, Loffler 1974). The rationale for their use is that the oxygen-free periods, characteristic of the monimolimnion of meromictic lakes, would preclude the development of benthic organisms such as chironomids. Their headcapsule remains would therefore not be found in the monimolimnetic sediments, unless they had washed in from above.

Several factors must be considered before fossil chironomid remains can be used as an indicator of meromixis in paleolimnological studies. First, with respect to living chironomids, it is essential to know what environmental factors are most important in influencing their abundance and distribution within the littoral and profundal zones of lakes. The literature suggests that oxygen (Bay *et al.* 1966), substrate type (Johnson *et al.* 1968) and food (Koskinen 1969, Dermott *et al.* 1977) are all important controlling variables.

Secondly, in order to make decisions about past events, it must be determined whether the fossil record at a particular location within the lake (profundal zone) is representative of the living chironomid population that existed at that location when the fossils were laid down. Resuspension rates of littoral chironomid forms, for example may vary through time, thereby generating erroneous conclusions about past organismal distributions. This misinterpretation of the fossil record may in turn result in an incorrect evaluation of paleo-environmental conditions.

Lastly, changes in productivity levels within a lake, with respect to food availability, may in turn alter the size and species composition of the resident chironomid population (Warwick 1975). Consequently, during the development of a lake, a change in total chironomid remains may reflect a change in the abundance and availability of food. Paleolimnologists must therefore learn to distinguish such food induced changes from those induced by meromixis, if fossil chironomids are to prove a useful indicator of the onset of meromixis. Likewise, methods of estimating rates of secondary transport must also be employed before the fossil chironomid abundance in the monimolimnetic sediments can be used as indicators of past periods of meromixis.

B. SEDIMENT DISTURBANCES

Sediments deposited on a lake bottom may be either mixed, or transported and redeposited or left undisturbed. Fossil record interpretation of a lake's developmental history requires the consideration of these three possibilities. In most lakes, extensive mixing of old and recent sediment particles occurs as a result of the burrowing habits of some benthic organisms (Brinkhurst 1974, Cole 1953, Berg 1938). The extent of mixing, coupled to sedimentation rates, will determine the resolution of the chemical, biological and physical stratigraphy. If sedimentation rates are low and vertical mixing is extensive, then sampling at very close vertical intervals (e.g., 5 cm) will not provide the refined chronological changes anticipated. In dealing with long-term trends with sampling intervals spaced 5 cm or more apart, mixing may be advantageous in that seasonal differences will have a tendency to be averaged out over a number of years. The littoral sediments in most lakes have a greater probability of mixing than do profundal sediments, and sediment mixing when it occurs will do so to a greater degree. This is a consequence of both the water depth and the amount of biological activity that occurs in the littoral zone relative to the profundal zone.

Davis (1968, 1973), using pollen grains as tracers, has shown that sediments are resuspended and redeposited resulting in a movement of the sediment from shallower to deeper parts of the lake. At present there is some controversy as to the extent of littoral chironomid headcapsule redeposition in the profundal zone. Iovino (1975), compared the mean annual larval population densities of several chironomid species with the number of their remains and found that there was relatively little movement of littoral remains into the profundal zone. Carter (1976, 1977) also found that the species composition of headcapsules in surface cores from Lough Neagh was similar to that of the living community. On the other hand, Lawrenz (1975) found headcapsules of littoral species in his profundal core, suggesting that some redeposition does occur, though to what extent we do not know at present. Hoffman (1971) found similar results which were associated with redeposition of littoral sediments during the low water stage in the Sub-Boreal. Deevey (1942), according to Stahl (1969), states that the great diversity of the chironomid remains in the profundal sediments, compared to the living fauna, suggests that redeposition of littoral chironomid remains occurs. Hence, redeposition of littoral sediments in the profundal zone may obscure a lake's developmental record. In this study, it is essential that very little, if any, redeposition occurs if total chironomid remains are to be used as an indicator of meromixis.

C. IRON AND MANGANESE

The abundance and distribution of iron and manganese in lake sediments depends upon their concentration in the drainage area, erosion intensity and conditions present in the deep waters during and after deposition.

Iron and manganese may be transported to a lake as either erosional material or as a result of their direct solution in the drainage basin (Kjensmo 1968a). If the former occurs then the iron to manganese ratio would remain similar to that found in the lithosphere (approximately 50:1), as erosion alone would not be expected to bring about any separation of the two elements. This relationship is exhibited in the glacial clays of a large number of sediment cores (Mackereth 1966, Kjensmo 1968a, Boyum 1976). During a lake's development, however, the sedimentary material eroded from the watershed may be diluted by organic matter and carbonaceous material. Also, preferential leaching of manganese may occur in the watershed. Therefore, in most cores, the high lithospheric iron to manganese ratios found in the glacial clay do not persist throughout the entire core.

The preferential migration of manganese may be brought about by soil reducing conditions of sufficient intensity to produce manganous ions yet not intense enough to effect large scale reduction of iron to ferrous ions. This would result in a decrease in the relative abundance of iron to manganese entering the lake. If the water column contains sufficient dissolved oxygen (>1 ppm), then the redox-potential (Eh) will be relatively high (300-500 mV) and both iron and manganese will precipitate out. If a low (<100 mV) redox-potential exists, then the ions will remain in solution.

Once iron and manganese have been deposited in the sediments, there are several factors that will affect their distribution and relative abundance. An iron and manganese-rich particle flow from the littoral zone into the profundal zone may occur. In Lake Mendota, Delfino et al. (1969) found a positive correlation between concentrations of iron and manganese and the depth of water where the samples were collected. It was assumed that Fe and Mn were carried to the deeper part of the lake, bound to small particles, by natural grading processes.

The redox-potential (Eh) of lake sediments and their overlying water, influences the solubility of various chemical substances, and their direction of movement across the mud-water interface. Mortimer (1941, 1942, 1971) clearly demonstrated that as the redox-potential decreases, the release of iron and manganese from the sediment increases markedly. A high redox-potential on the other hand, prevents the significant release of soluble components from the interstitial waters of the sediment to the overlying water. The iron and manganese that diffuse into the water may be carried into the upper water layer and thus removed from the lake, or they may be reprecipitated. The process which occurs depends upon both the velocity of the circulation and the flow through rate in the lake (Boyum 1976).

Should the Eh continue to decrease below 100 mV, sulfate will be reduced to hydrogen sulfide. If ferrous iron is present in the water in relatively large quantities, FeS may form. Since this compound is insoluble, it will precipitate out, re-enriching the sediments with iron. Manganese will continue to decline in concentration. If there exists a permanently stagnant layer, as in the monimolimnion of meromictic lakes, then a constant drain of manganese from the sediment into the hypolimnetic waters and a sediment iron enrichment (as FeS) will occur. This will result in an increase in the Fe:Mn ratio of the sediment.

Kjensmo (1968b) postulated that an increase in the sedimentary Fe:Mn ratio may be an indicator of the onset of meromixis. During the development of Lake Svinsjoen, sediment iron and manganese concentrations showed a very marked maximum, while the lowest iron to manganese ratio in the entire core prevailed prior to the meromictic period. Mackereth (1966) has also used the increase in the Fe:Mn ratio as an index to show the progression from oxidizing to reducing conditions in the hypolimnion of several lakes in the English Lake district.

During the meromictic period of a lake's history, Boyum (1976) found a much higher iron to manganese ratio than during the lake's holomictic period. The meromictic period was characterized by a very large iron concentration (19% of dry weight of the sediment), in contrast with its holomictic period (5%). Consequently, from Boyum's and Kjensmo's studies, it would appear that a relatively low Fe:Mn ratio prevails before and after meromixis.

3. PIGMENTS

In lake sediment, a seasonal deposition of photosynthetic material from allochthonous and autochthonous sources occurs. In time, though relatively few morphological remains persist in the sediments, their fossil pigments remain as an indication of their prior existence (Vallentyne 1960, Brown 1969, Wetzel 1975). Specific pigments have been associated with particular groups of organisms and events in a lake's development (Brown 1968, Czeczuga and Czerpak 1968). The appearance of oscilloxanthin in sediment cores has been used to indicate the invasion of blue-green algae in association with recent eutrophication (Brown and Coleman 1963, Griffiths *et al.* 1969).

Vallentyne (1955) suggested that fluctuations in total sedimentary chlorophyll degradation products (SCDP) along a core may be used to infer changes in the abundance of plant material. Numerous investigations since Vallentyne's study have interpreted stratigraphic changes in SCDP as representing changes in lake productivity (Fogg *et al.* 1961, Belcher *et al.* 1964, Czeczuga 1965, Wetzel 1970, Sanger and Gorham 1972, Whitehead *et al.* 1973, Gorham and Sanger 1976). Its use however is somewhat speculative.

Considerable discussion has occurred with respect to the validity of using SCDP units as an index of past conditions of plant productivity and lake trophy (Gorham, 1960, Moss 1968, Daley 1974, Daley *et al.* 1977). The concentration of surficial sediment chlorophyll degradation products in relation to total organic matter has been shown to be closely correlated to present trophic conditions (Gorham *et al.* 1974). More recently, however, Daley *et al.* (1977) provided evidence that serious errors may occur in measuring SCDP values due to variation in α-phorbin components, inferference by β-phorbins and possible variation by non-phorbin contaminants. It is accepted, however, that in association with other parameters, SCDP units are useful, though much caution must be used in interpretation of the data.

The validity of using SCDP units depends primarily on the preservation of the pigments, the extent of differential degradation during and after sedimentation and the extent of allochthonous sources of sedimentary pigment degradation products (Adams et al. 1976). According to Wetzel (1970), the anaerobic monimolimnetic sediments of meromictic lakes should preserve pigments exceptionally well because of the lack of light, low temperature and lack of oxygen which prevail there. Gorham and Sanger (1972) in support of Wetzel's contention found that the monimolimnetic (profundal) sediments in Stewart's Dark Lake contained higher pigment concentrations that did the littoral sediments.

Daley et al. (1977), found that pigment values in the sediment of meromictic Little Round lake were only half those found by Gorham and Sanger (1972) in meromictic Stewart's Dark Lake. Hence large differences in the profundal sediment fossil pigment concentration can be expected between meromictic lakes. Presumably, this is a consequence of productivity differences between lakes. Ultimately, however, such variability may obscure statistical differences between holomictic and meromictic lakes.

Other factors are important in determining the quantity of pigments present in sediments. Studies with respect to the distribution and decomposition rates of plant pigments in woodland soils, swamps, ponds and lakes indicate, that in unproductive lakes, allochthonous sources contribute more to the sediments than autochthonous sources. Hence plant pigments in the sediments of unproductive lakes are present in lower concentrations than those found in highly productive lakes. In productive lakes, the opposite is true (Gorham and Sanger 1964, 1967). The reason for this is that pigments from allochthonous sources, in contrast with those from autochthonous sources, undergo extensive degradation before entering the lake. For fossil pigments to be a useful paleoindicator of meromixis, it is imperative that pigment source variability-induced changes are negligible relative to changes induced through increased preservation.

Paleolimnologists have argued that observed changes in the Fe:Mn ratio and changes in fossil chironomid headcapsule abundance can indicate the initiation of meromixis. Furthermore, it has been implied in the literature, though never formally stated, that increases in plant pigments may occur with the initiation of meromixis due to increased preservation. To date however, no comparative study has been done on surficial sediments to show whether the assumed relationship does in fact hold true.

The objectives of this study were threefold; first to determine if a significant difference between the two lake types occurred with respect to their Fe:Mn ratios, total number of fossil chironomid headcapsules, and the preservation of plant pigments. Secondly, to determine whether all variables studied supported each other with respect to the developmental changes in Crawford lake. Lastly, changes in the profundal zone may reflect changes in the littoral zone, especially with respect to the total number of headcapsules and the concentrations of plant pigments. Hence, littoral to profundal zone ratios were compared assuming that this procedure would reduce between-lake differences within each lake type.

II. MATERIALS and METHODS

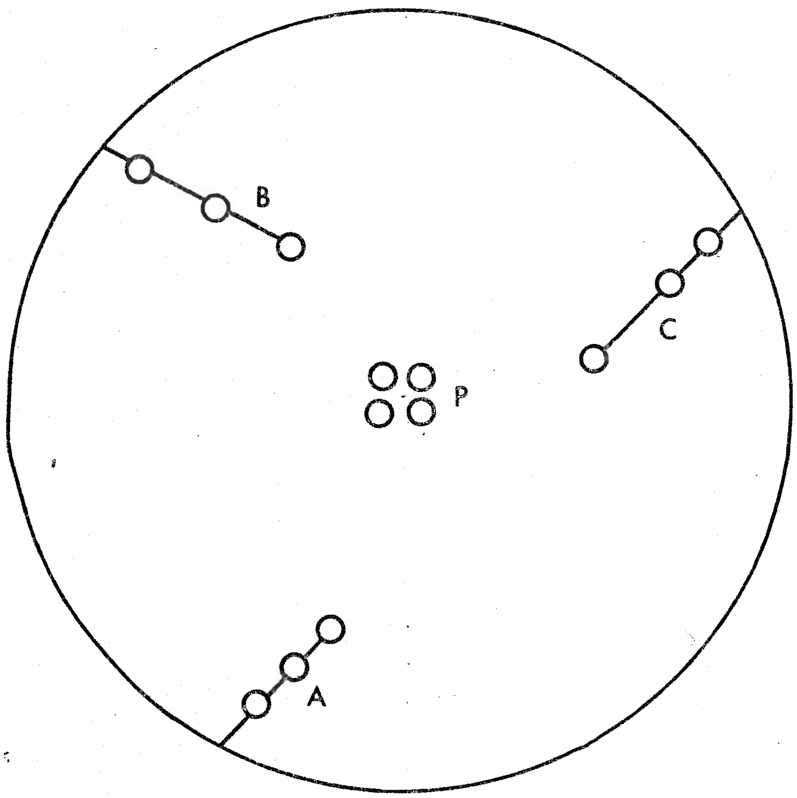
A. SAMPLE COLLECTION

In a study of this type there are two approaches that may be used with respect to data collection. The first involves the use of a very small number of lakes (*e.g.*, 2 lakes, 1 meromictic and 1 holomictic) that are cored very intensively (*e.g.*, 50 cores per lake). The question that arises from this type of study is whether or not the two lakes selected were truly representative. This is especially true when one considers the great variation in trophic status between lakes and consequently the length of time anaerobic conditions would prevail in the profundal zone of these holomictic lakes.

The second approach, the one used in this study, involved the sampling of a greater number of lakes (10) that were cored less intensively (12-16 cores per lake). Sediments from different cores collected along the same transect were combined, thus providing 2 or 3 composite littoral transect samples per lake. Combining all transect cores into one composite sample was felt to be necessary in order to maintain the number of samples within a manageable size. The littoral zone transects were then averaged to give a single pooled littoral value for each lake. This provided a basis on which a single comparison could be made with the single profundal value (Fig. 1). The consequences of this are discussed on pages 63, 67, and 90 of this thesis.

Surface sediment samples were collected using a K-B gravity corer (Brinkhurst *et al.* 1969) during the summer of 1976. Samples were obtained

Figure 1. Representation of sampling and pooling techniques for littoral cores



$$\frac{A+B+C}{3} = L$$

from both the profundal and littoral zones of four meromictic and six holomictic lakes. Four profundal cores were taken in close proximity to each other (i.e., within 3 m of the deepest part of each lake). Littoral cores were collected along a series of transects consisting of two or three transects per lake. Inflow and outflow regions were excluded in selecting transect sites, as the sediments were more apt to be disturbed in these areas and consequently less representative of the littoral region as a whole. With the exception of Pinks lake, each transect consisted of three or four cores collected at different depths. Most of the littoral sediments in Pinks lake were too hard to permit sampling with a K-B corer.

The sediment cores were extruded in the field after the overlying water had been carefully siphoned off. The top fifteen centimetres of sediment were stored in plastic bags and returned to the laboratory for later analysis.

In the laboratory, all sediment samples from a single transect were combined and slowly homogenized for fifteen minutes using a Waring commercial blender, controlled by a Variac autotransformer (type W5MT3, General Radio Company). The same procedure was applied to all samples collected within the profundal zone of a particular lake. Appropriate sized subsamples (as described below) for various physical, chemical and biological analyses were removed and dark-stored in plastic vials at 4°C, until treated according to the procedure outlined in the following chemical analysis section. The samples to be analyzed for plant pigments were frozen rather than stored at 4°C.

On March 10, 1976, a modified Livingston corer (Wright et al. 1965) was used to remove a 4.25 metre long core from the deepest part (20 m) of

Crawford lake. The core sections were returned to the lab in their metal casings and extruded the following day. The core was sectioned into 5 cm long lengths and dark-stored at 4°C. All analyses utilized the same methods as were employed on the surface sediments.

B. CHEMICAL ANALYSIS

1. Water, Organic Matter and Carbonate Contents

To determine the water content of the sediment, triplicate 2 ml samples of homogenized sediment slurry were dried at 95°C for 24* hours in pre-weighed ceramic crucibles. After cooling to room temperature in a desiccator, the samples were reweighed. The sample water content was calculated by subtracting the dry weight from the initial weight.

The organic matter was determined by ashing the samples described above. The dry sediment samples and crucibles were placed in a muffle furnace, heated to 550°C for one hour, cooled and reweighed as above. The difference between this weight and the dry weight represents the amount of organic carbon ignited (Dean 1974). The weight loss on ignition was expressed as a percent relative to the dry weight of the sediment.

Carbonate was determined by returning the samples to the muffle furnace after ashing, and heating them to 1000°C for one hour. The weight loss between 550° and 1000°C represents the amount of CO_2 evolved from carbonate minerals (Dean 1974). All my weighings were done on a Mettler HF type balance at a precision of ±0.1 mg.

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* A twenty-four hour drying period at 95°C has been shown to be sufficient to remove the water in both organically rich and organically poor sediments (See Appendix A).

2. Sediment Digestion

Initially, fresh sediment samples were oven dried at 65°C for 96 hours, ground and passed through a 180 μm mesh sieve. Two to five replicates for each sample location were digested, and later analyzed for total iron and manganese. The sediment was brought into solution using standard nitric-perchloric acid digestion techniques as described below.

Sample aliquots of approximately 0.5 g were placed in 30 ml polypropylene beakers and heated directly on a hot plate for about 12 hours in the presence of 20 ml of 47% hydrofluoric acid (Mackereth, 1966). The solid residue which resulted was rinsed into a 125 ml erlenmeyer flask with distilled water and subsequently heated until the volume had been reduced to about ten ml. Five ml of concentrated nitric acid was added to the cooled flasks which in turn were covered with a watch glass and heated at medium heat until a large proportion of the organic matter had been visibly destroyed (approximately 12 hours). The samples were then cooled to room temperature, 3 ml of 70% perchloric acid added, and reheated until all the organic matter was destroyed. The digested samples were then evaporated to dryness and the resultant precipitate was dissolved in 3 ml of concentrated hydrochloric acid. Twenty ml of distilled water was added and the diluted acid solution was then filtered through a pre-rinsed Whatman No. 1 filter. The filtrate was drained directly into a 50 ml volumetric flask which was later brought to volume (50 ml) by adding distilled water. This solution was then stored in glass vials at 4°C in the dark. Appropriate sized subsamples were then used for the total iron and manganese determinations.

Total iron was determined by the orthophenanthroline method (Standard Methods, 1971) while manganese determinations were made by direct aspiration of the digested solution into a Perkin-Elmer model 403 Atomic

Absorption Spectrophotometer. For both iron and manganese, a standard curve was plotted. Suitable subsamples were used so that the readings occurred within the linear region of the standard curve. The results were expressed as a percentage of the dry weight and the organic weight of the sediments.

C. CHIRONOMID HEADCAPSULES

The extraction of fossil chironomid headcapsules was accomplised by taking (in triplicate) five to ten ml aliquots of the freshly homogenized sediments which were placed in plastic vials and freeze-dried. Each freeze-dried sample was transferred to a 100 ml beaker, heated to near boiling in 10% (w/v) KOH for one to two hours and then washed through a series of three seives with mesh sizes of 0.250, 0.180 and 0.125 mm. The chironomid headcapsule residues from each sieve were in turn washed into a scored petri dish and counted at 45X magnification using a Leitz binocular dissecting microscope. As each intact headcapsule was counted, it was removed from the residue and mounted (ventral side up) on a glass slide in Hoyer's Solution. The number of headcapsules counted varied between 0 and 80 per 10 ml sample, depending upon their density in the sediment. The results were expressed relative to both the dry weight and organic weight of the sediment.

D. PIGMENT EXTRACTION

Sediment samples were frozen within 24 hours after collection and dark-stored until they could be analyzed for chlorophyll, carotenoids and their degradation products. In some cases, samples were stored for up to ten months before pigment extraction could be performed. Sample storage time should have no appreciable effect on sediment pigments and their degradation products (Vallentyne 1955).

The frozen samples were dark-thawed at 4°C, and mixed by vigorous shaking. One to ten gram samples were placed in pre-weighed 30 ml Corex centrifuge tubes and centrifuged to remove excess water. The size of the aliquot used varied inversely with the pre-determined organic matter content of the sediment.

Approximately 5 ml of 90% acetone-water (v/v) was added to the samples which in turn were mixed in a Vari-Whirl mixer (VWR Scientific Co.) for approximately one minute. The resultant acetone-pigment solution was centrifuged for ten minutes at 7000 rpm in a clinical centrifuge (IEC Company) and the supernatant liquid was decanted and stored in 125 ml Erlenmeyer flasks. This was repeated until the supernatant liquid contained no visible coloration. Generally, 60 to 160 ml of acetone was required, depending upon the amount of pigment present in the sediment. The pigment acetone solution was filtered through a Whatman glass fibre filter, brought up to a known volume, in a graduated cylinder, and then dark-stored at 4°C until absorbance readings could be taken (within 96 hours). All pigment extractions were performed in the laboratory at room temperature.

Measurements of absorbance were made using a Hitachi double beam spectrophotometer at or near 667 nm for chlorophyll derivatives and at 450 nm for carotenoids (Sanger and Gorham 1972). As extraneous compounds may contribute to absorbance at the red peak for chlorophyll derivatives (Orr and Grady 1957, Gorham 1960), a correction for background absorbance at 750 nm (Wetzel 1970) was subtracted from the chlorophyll peak.

Pigment concentrations were expressed as units per gram of organic matter and as units per gram dry weight of sediment. One unit was equivalent to an absorbance of 1 in a 10 mm cell when dissolved in 10 ml of solvent (Vallentyne 1955). Expressing the pigment concentrations relative to the organic matter avoided distortion of the pigment concentration by inorganic materials in the sediments.

E. PHYSICAL CHARACTERISTICS

In July 1977, morphometric maps were constructed for White Duck and Canoe lake based on ten transects per lake. Depths were recorded using a Garcia recording depth sounder.

The volume, mean depth, surface area and shoreline development for each lake were determined using polar planimetry (Lind 1974). Morphometric maps were obtained from various sources for the remaining lakes used in this study (Appendix B).

F. STATISTICS

Siegel (1956), Snedecor and Cochran (1967) and Harshbarger (1971) were used as statistical references throughout the research. Hypotheses involving meromictic and holomictic surface sediment differences were tested using the Mann Whitney-U test. Full statistical significance was achieved when the probability (p) (one-tail) of obtaining a particular result in a given test, under the null hypothesis was ≤ 0.05.

Correlation coefficients were determined using stepwise linear regression for each set of paired variables in the Crawford lake profundal core. In this analysis, it was difficult to designate what constituted a totally independent sample, hence, the smallest n (number of variables) was used in evaluating whether full statistical signficance was achieved, rather than the total number of replicates.

III. RESULTS

A. SURFACE SEDIMENTS

1. Lakes

The location of all lakes sampled during this study and their morphometric characteristics are shown in Figure 2 and Table 1, respectively. Morphometric maps for each lake (excluding Found, which was unavailable) have also been included (Figs. 3-10), with the approximate location of each littoral core indicated.

For each lake, mean summer Secchi transparency depth was plotted against mean profundal chlorophyll SPDU's (Fig. 11). A near significant correlation ($r = 0.657$, $p = 0.053$) resulted. Canoe Lake was eliminated from this analysis due to its dystrophic nature, as was Found Lake due to the water clarity (see Carlson 1978). Sunfish Lake, though not included in the other analyses, was included in this data set. Generally those lakes with the greater depth of light penetration contained the least amount of chlorophyll in their profundal sediments.

2. Organic Matter

The organic matter in littoral and profundal sediments as determined by weight loss in ignition was quite variable, both within and between each lake type (Table 2). In the littoral sediments of the meromictic lakes, percent organic matter ranged from a low of 6.3% (Pinks' Lake) to a high of 30.9% (Little Round Lake). In the littoral sediments of the holomictic lakes, percent organic matter varied from 6.2% for the dystrophic

Figure 2. Map of Southern Ontario

showing the location of all meromictic (●) and holomictic (o) lakes sampled in the study

Lake number	Lake
1	Little Round
2	Pinks
3	Crawford
4	McGinnis
5	St. George-1, 2
6	Coon
7	Found
8	Canoe
9	White Duck

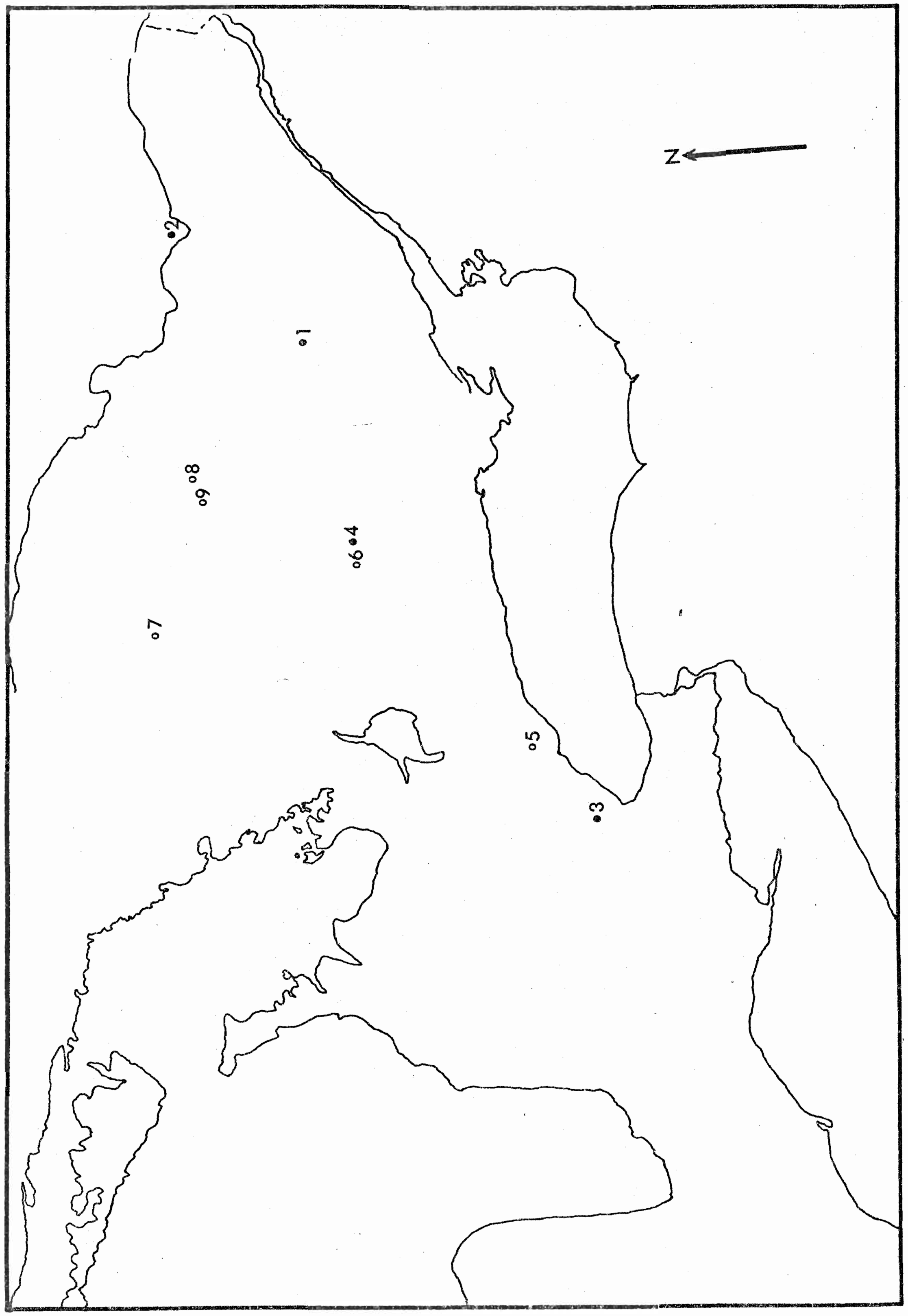

N
1
2
3
4
5
6
7
8
9

Table 1. Latitude, longitude, lake surface area (A_0), mean depth (Z), lake volume (V), shoreline length (L), shoreline development (D_L) and maximum length (L_{max}) of lakes sampled in this study.

Lake	Latitude (°N)	Longitude (°W)	A_0 (km^2)	Z (m)	V ($m^3 \times 10^6$)	L ($m \times 10^3$)	D_L	L_{max} (m)
Meromictic								
Little Round	44° 47'	76° 41'	0.074	8.14	0.61	1.03	1.07	480
Pinks	45° 27'	76° 48'	0.118	12.7	1.50	1.89	1.55	781
Crawford	43° 28'	80° 57'	0.024	10.4	0.25	0.64	1.17	264
McGinnis	44° 36'	78°2.5'	0.048	6.2	0.30	1.15	1.48	367
Holomictic								
St. George-1	43° 57'	79° 26'	0.049	6.2	0.31	0.99	1.26	831
St. George-2	43° 57'	79° 26'	0.042	4.3	0.18	0.80	1.10	253
Coon	44° 36'	78° 12'	0.347	4.0	1.39	4.56	2.18	1286
Found	45° 33'	78° 39'	0.130	11.6	1.50			
White Duck	45° 21'	77° 41'	0.193	3.5	0.68	2.34	1.50	700
Canoe	45° 21'	77° 36'	0.179	3.8	0.67	1.77	1.18	650

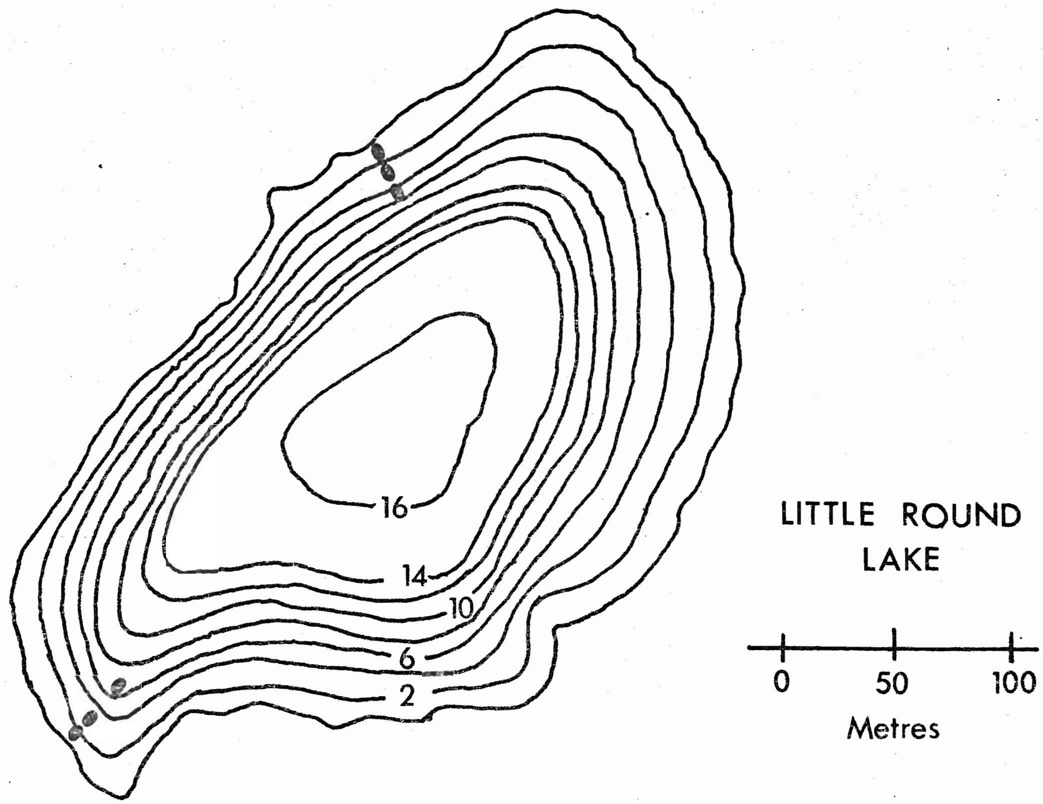


Figure 3. Morphometric map of Little Round Lake

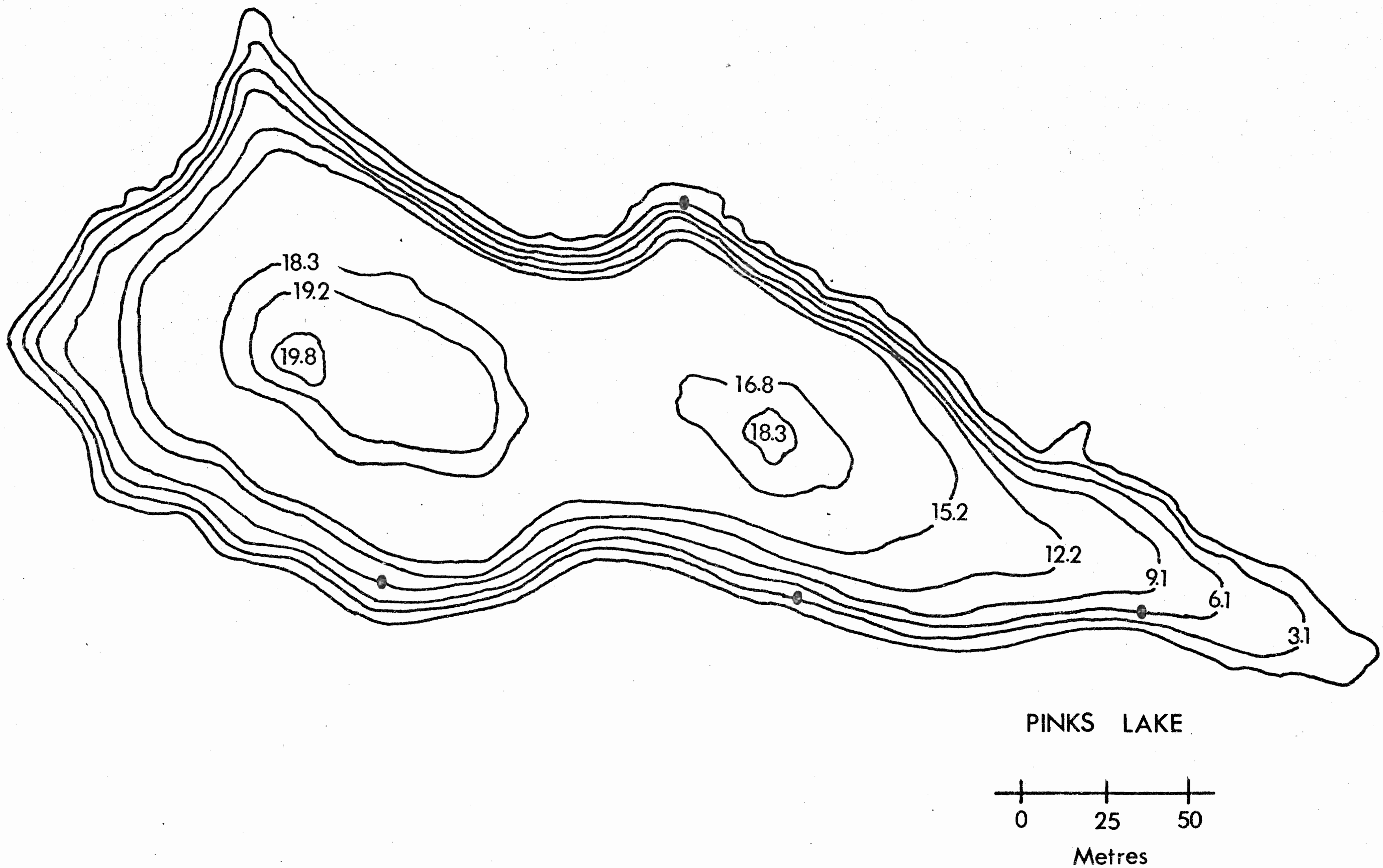


Figure 4. Morphometric map of Pinks Lake

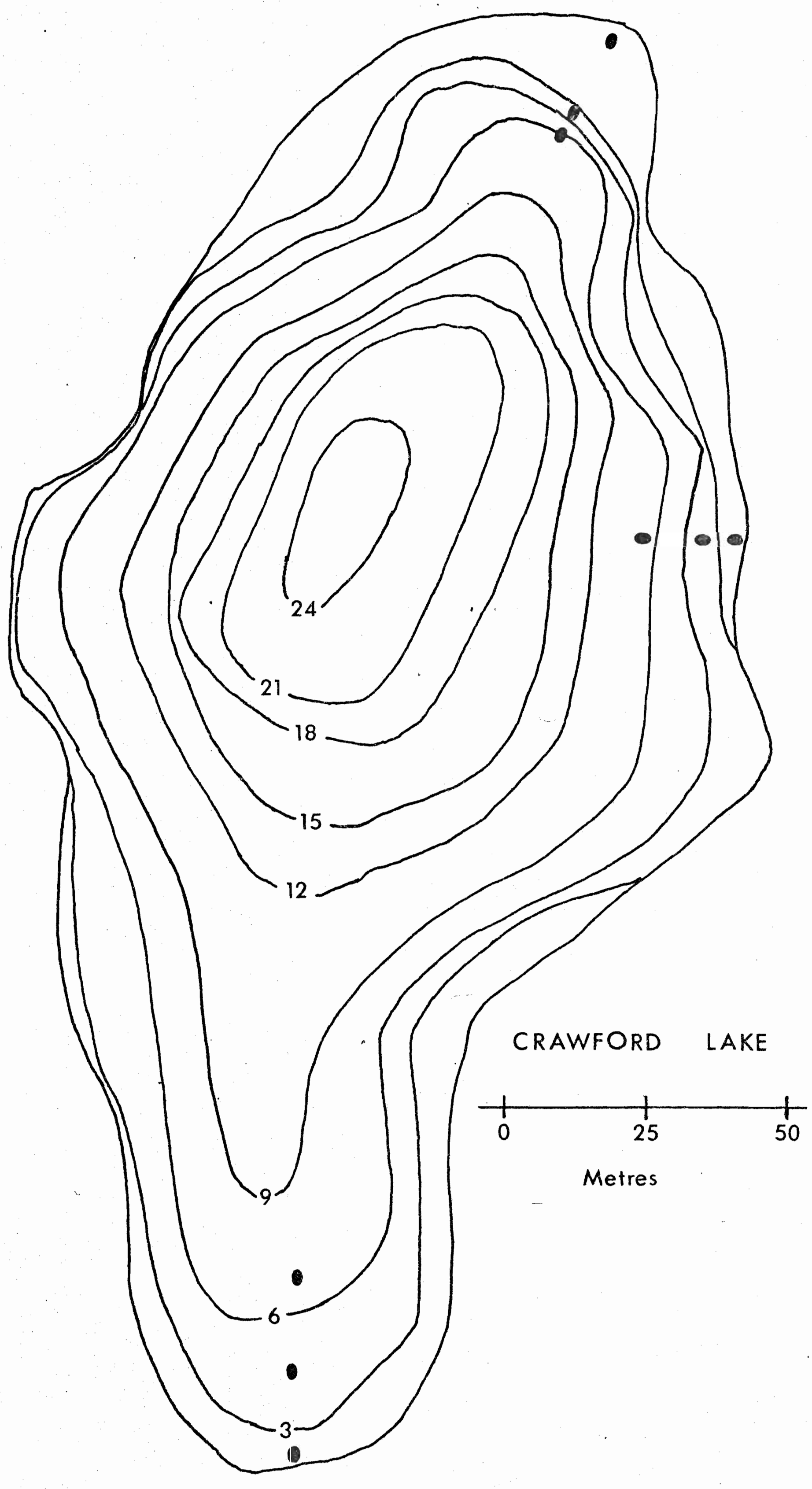


Figure 5. Morphometric map of Crawford Lake

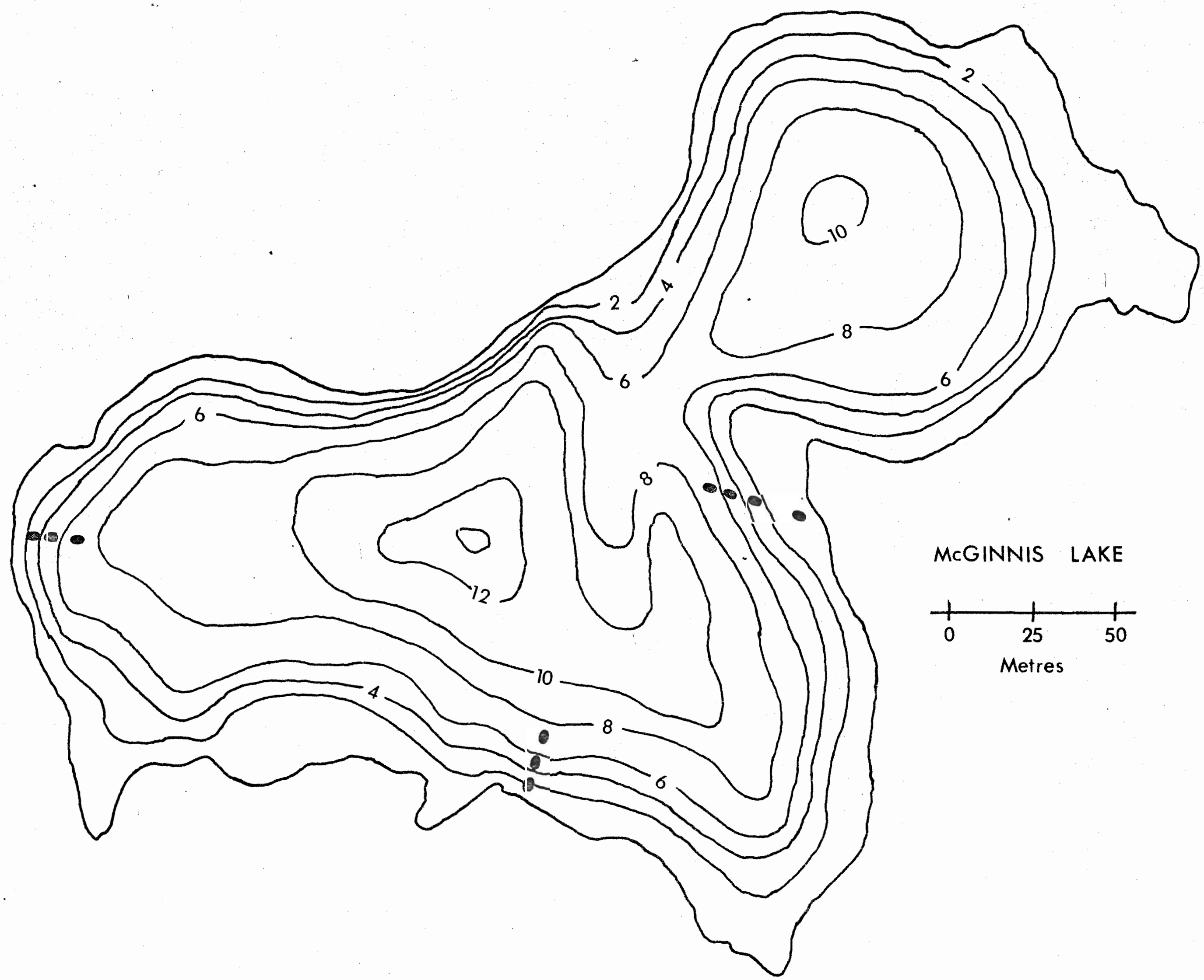


Figure 6. Morphometric map of McGinnis Lake

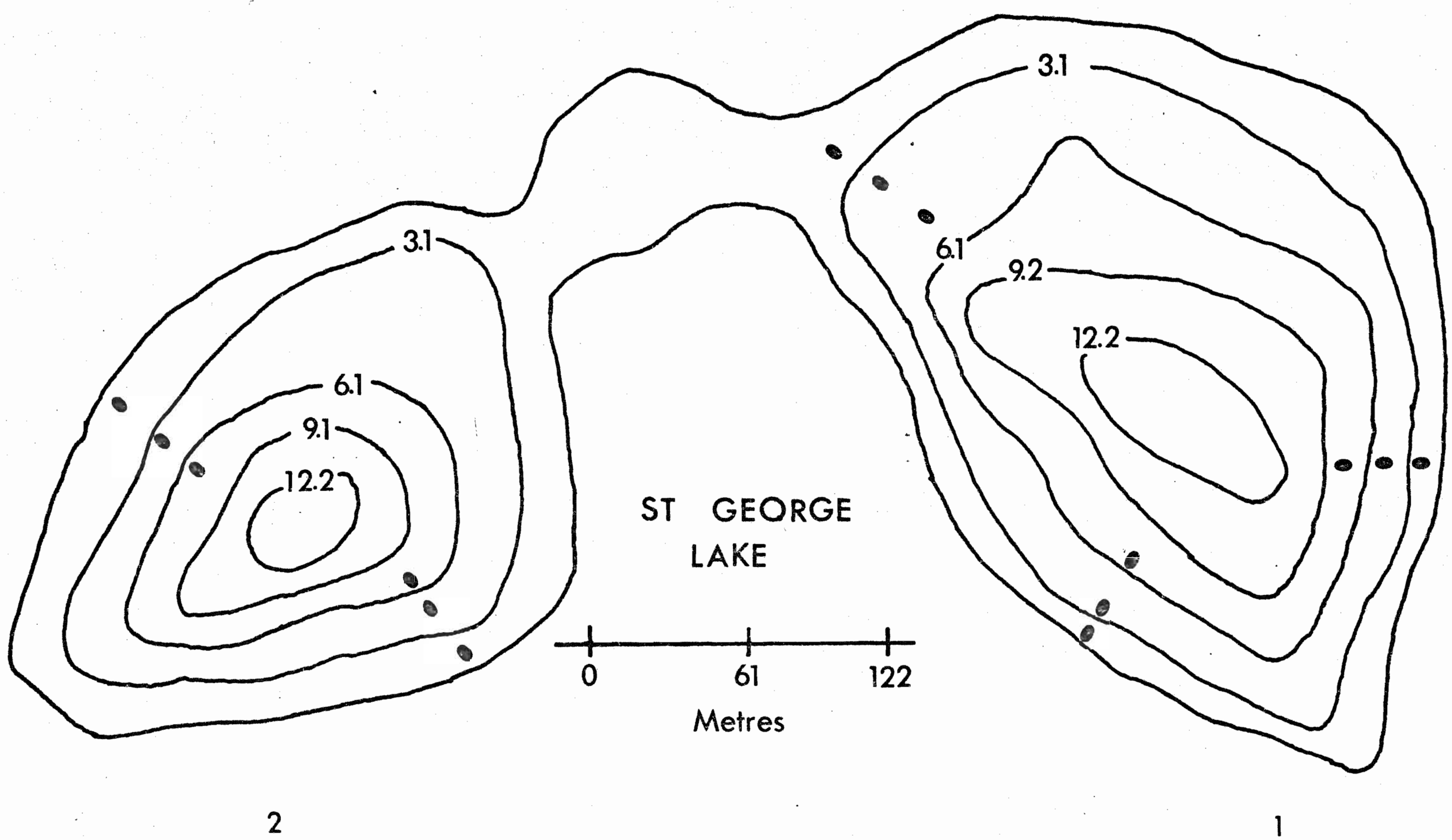


Figure 7. Morphometric map of Lake St. George-1, 2

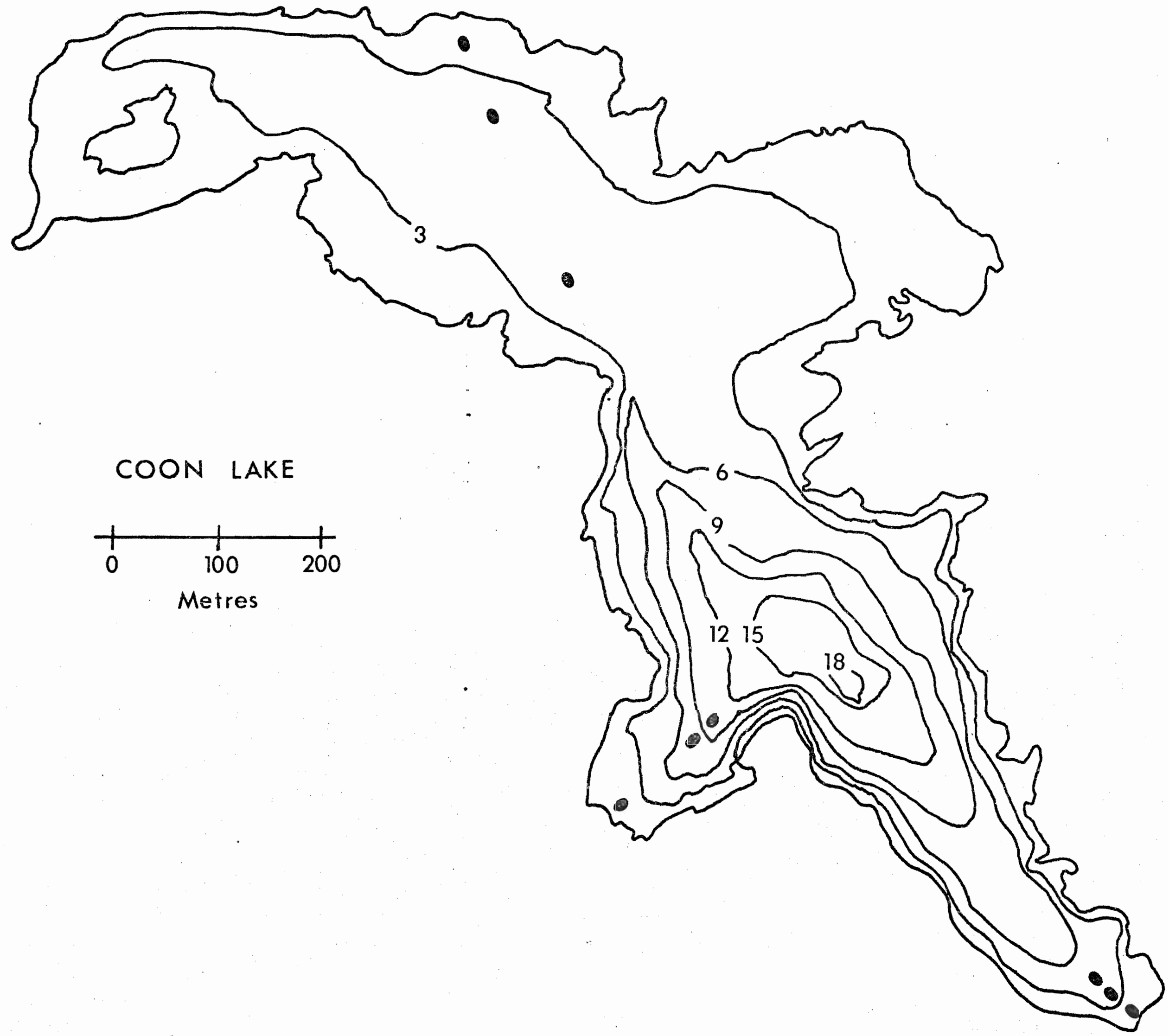


Figure 8. Morphometric map of Coon Lake

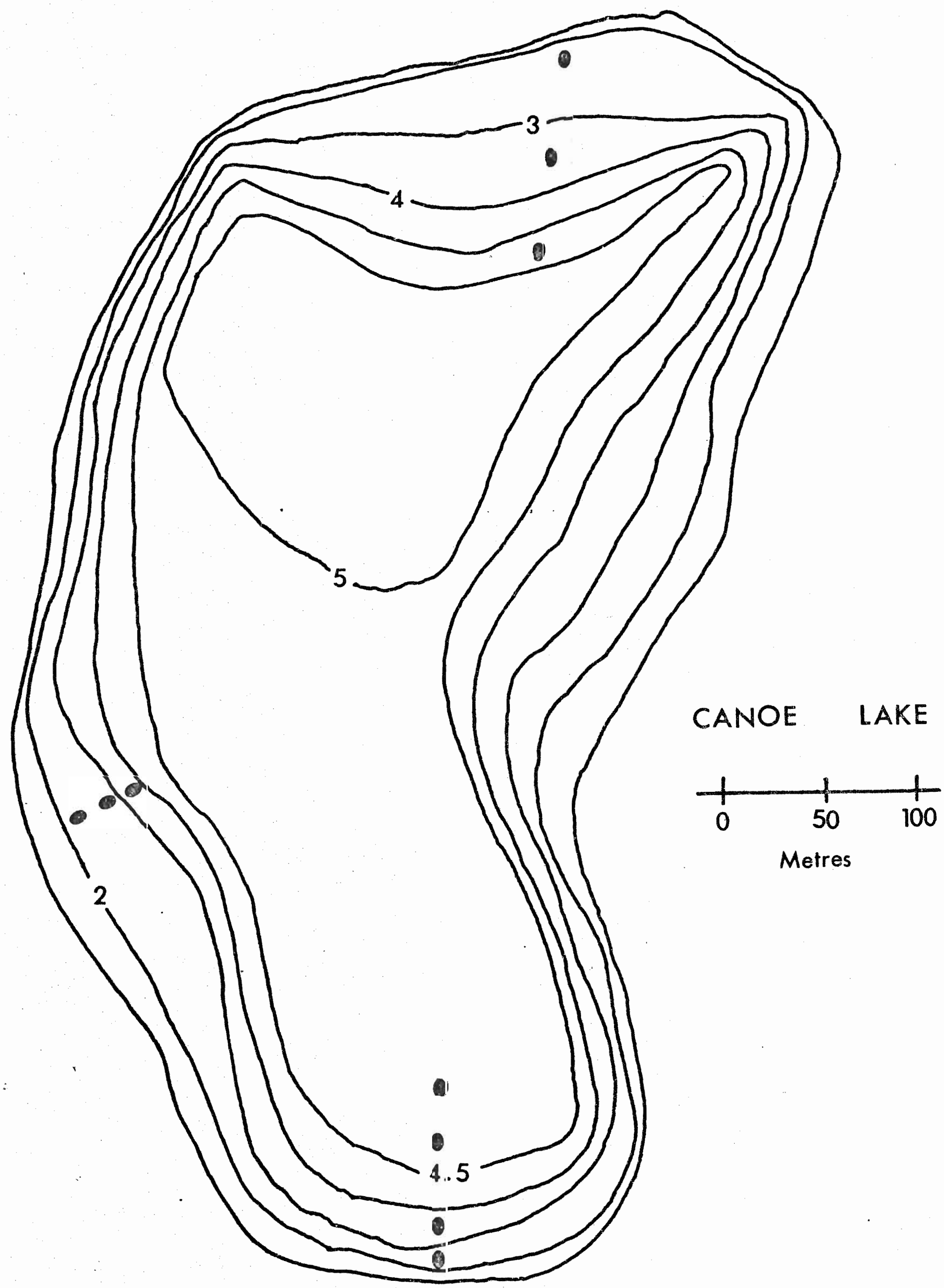


Figure 9. Morphometric map of Canoe Lake

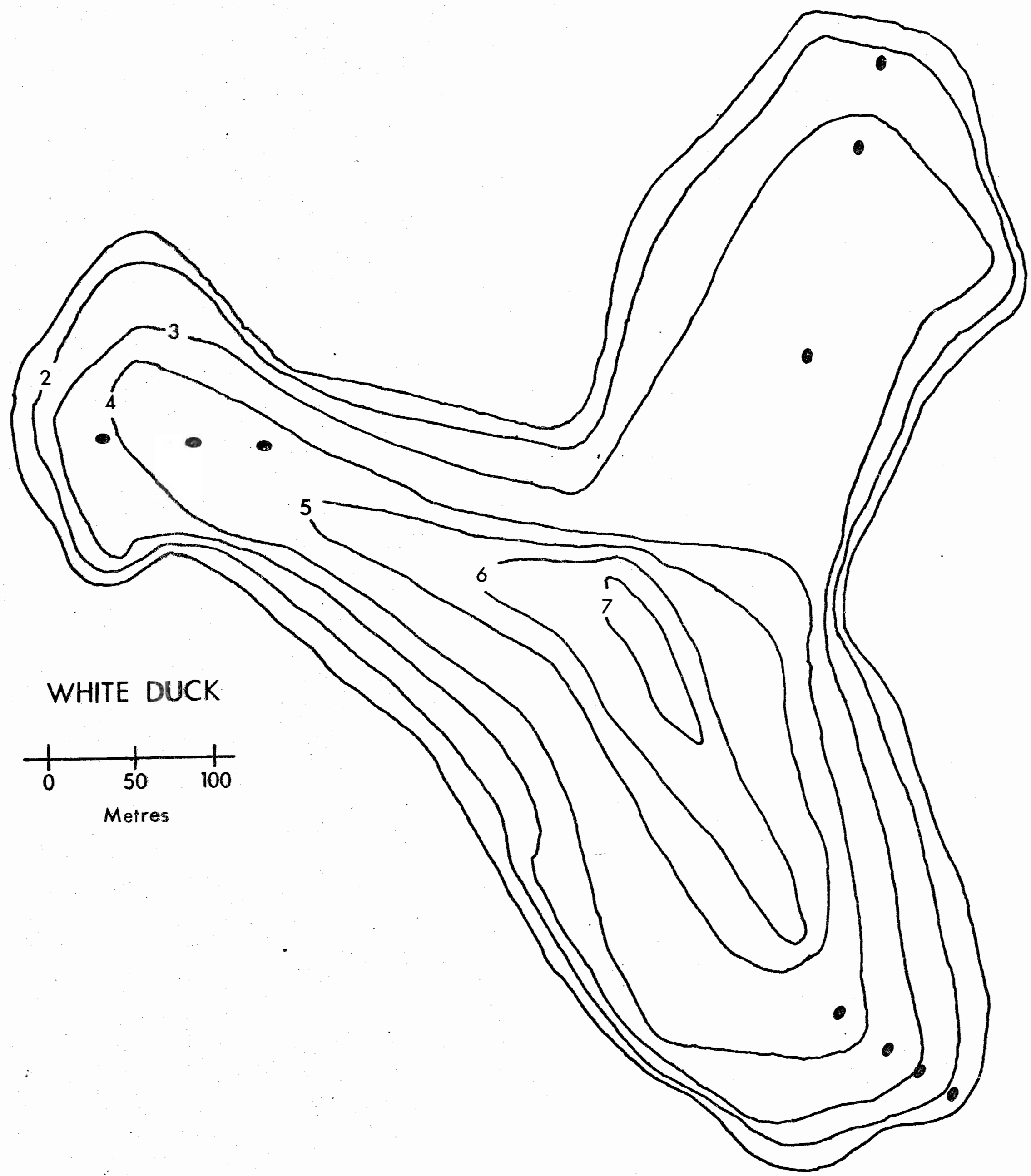
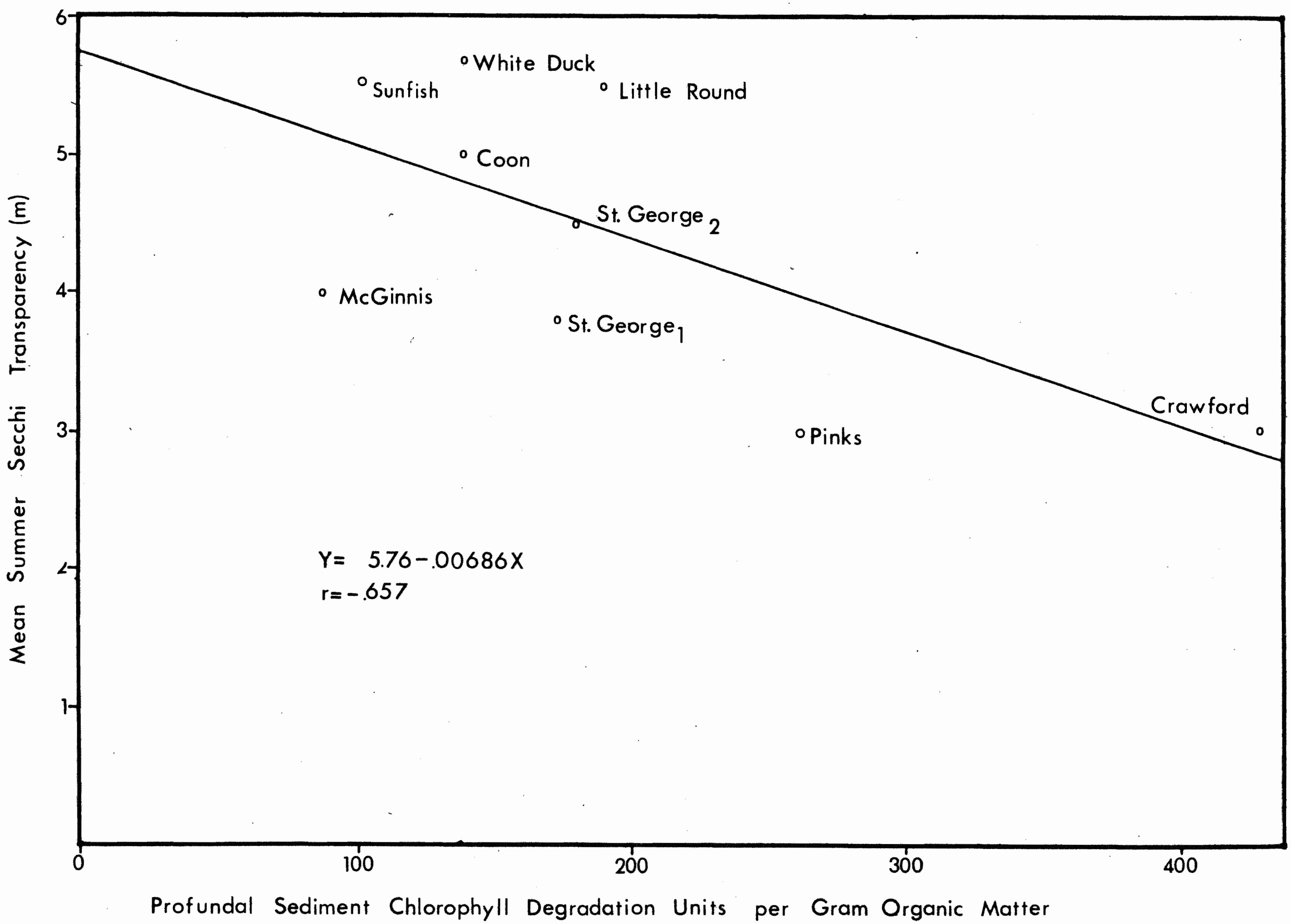


Figure 10. Morphometric map of White Duck Lake

Figure 11. Regression line fitting the relationship between mean Secchi transparency and profundal sediment chlorophyll degradation products.



Mean Summer Secchi Transparency (m)
Profundal Sediment Chlorophyll Degradation Units per Gram Organic Matter
0
1
2
3
4
5
6
100
200
300
400
White Duck
Sunfish
Little Round
Coon
St. George 2
McGinnis
St. George 1
Crawford
Pinks
Y= 5.76-.00686X
r=-.657

Table 2 Organic Matter Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Organic Matter as percent Dry Weight	Profundal Organic Matter as percent Dry Weight	Littoral/Profundal Ratio
Little Round	30.9	47.1	0.66
Pinks	6.3	46.7	0.13
Crawford	10.6	31.6	0.33
McGinnis	9.3	13.4	0.69
St. George-1	20.7	30.4	0.68
St. George-2	29.4	32.2	0.91
Coon	44.0	48.4	0.91
Found	7.6	44.7	0.17
White Duck	19.2	43.8	0.44
Canoe	6.2	33.9	0.18
U Value	12	11	9
Significance*	NS	NS	NS

*NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

Canoe lake to 44% for Coon Lake.

The profundal sediments of both meromictic and holomictic lakes examined in this study contained larger quantities of organic matter than did their respective littoral zone sediments. In meromictic lakes, profundal organic matter varied from 13.4% to 47.0% with a mean of 34.7% (std. dev. 15.9%). In holomictic profundal sediments, a low of 30.4% organic matter was found in St. George-1 and a high of 48.4% in Coon Lake with a mean of 38.9% (std. dev. 7.6%).

No significant differences were found with either the amount of littoral or profundal organic matter, or intra-zonal changes (littoral to profundal ratio) in organic matter between the meromictic and holomictic lakes studied.

3. Carbonate

Significant differences existed between the meromictic and holomictic lakes chosen in this study with respect to the percentage carbonate present in their littoral sediments. Generally, the littoral sediments of the meromictic lakes contained larger quantities of carbonate than those of the holomictic lakes. Little Round Lake was the only meromictic lake that contained less carbonate in its littoral sediments than several holomictic lakes (Table 3). In the meromictic lakes, carbonate ranged from a low of 12.4% (Little Round Lake) to a high of 37.0% (Crawford Lake). In the holomictic lakes, it ranged from 0.6% to 25.3% in Found and St. George-1 respectively.

The carbonate content of the profundal sediments was not significantly different between the two lake types. In meromictic lakes, it ranged from

Table 3. Carbonate Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Carbonate Content as percent Dry Weight	Profundal Carbonate Content as percent Dry Weight	Littoral/Profundal Ratio
Little Round	12.4	3.8	3.3
Pinks	28.1	3.5	8.0
Crawford	37.0	16.0	2.3
McGinnis	35.8	33.8	1.1
St. George-1	25.3	11.0	2.3
St. George-2	17.8	4.7	3.8
Coon	3.4	4.6	0.7
Found	0.6	2.9	0.2
White Duck	1.2	2.6	0.5
Canoe	0.8	3.8	0.2
U Value	2	7	7.5
Significance*	S	NS	NS

* S: Significant difference ($p \leq 0.05$) between meromictic and holomictic lakes

NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

3.5% (Pinks Lake) to 33.8% (McGinnis Lake). In holomictic lakes, the carbonate content ranged from a low of 2.6% (White Duck Lake) to a high of 11.0% (Lake St. George-1).

4. Iron

Littoral sediment iron concentration of the four meromictic lakes studied did not differ significantly from that of the six holomictic lakes, when expressed as mg of iron per g organic matter (Table 4). In meromictic lakes, the iron concentrations ranged from 13.5 to 103.8 mg Fe/g organic matter, as compared with 45.5 to 905.1 mg Fe/g organic matter in holomictic lakes. When the littoral sedimentation iron concentration was expressed as a percent of the dry weight of the sediment (Table 5), holomictic lake sediment iron concentration was significantly greater than that observed in meromictic lake sediments. In holomictic lakes, iron ranged from 12.0 to 56.5 mg Fe/g dry weight as compared to 1.3 to 18.2 in meromictic lakes.

In profundal sediments, when iron was expressed as a function of the dry weight of the sediment and as a function of the organic matter content, there was significantly less iron in meromictic lake sediments than in the holomictic ones (Tables 4 and 5).

No significant difference occurred between holomictic and meromictic lakes when iron was expressed relative to the organic matter content of the profundal *vs* littoral zone sediments (littoral to profundal ratio). Relative to the dry weight of the sediment, however, the iron content was significantly lower in meromictic lakes. It ranged from 0.26 to 0.70 as compared with 0.40 to 1.27 in holomictic lakes.

Table 4. Iron Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Iron Content as mg/g Dry weight	Profundal Iron Content as mg/g Dry Weight	Littoral/Profundal Iron Ratio
Little Round	18.2	25.9	0.70
Pinks	6.5	18.6	0.35
Crawford	2.1	7.9	0.27
McGinnis	1.3	4.8	0.26
St. George-1	12.0	22.3	0.54
St. George-2	13.4	33.4	0.40
Coon	28.1	38.2	0.74
Found	35.0	36.5	0.96
White Duck	30.2	23.8	1.27
Canoe	56.5	79.1	0.72
U Value	2	2	2
Significance*	S	S	S

* S: Significant difference ($p \leq 0.05$) between meromictic and holomictic lakes.

Table 5. Iron Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Iron Content as mg/g Organic Matter	Profundal Iron Content as mg/g Organic Matter	Littoral/Profundal Iron Ratio
Little Round	58.9	54.9	1.07
Pinks	103.8	39.7	2.61
Crawford	20.0	25.0	0.80
McGinnis	13.5	35.6	0.38
St. George-1	59.7	73.6	0.79
St. George-2	45.5	103.5	0.44
Coon	63.8	78.8	0.81
Found	461.1	81.6	5.65
White Duck	157.8	54.3	2.91
Canoe	905.1	233.2	3.88
U Value	5	1	8
Significance*	NS	S	NS

* S: Significant difference ($p \leq 0.05$) between meromictic and holomictic lakes.

NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

5. Manganese

The manganese content of the littoral sediments when expressed on either a dry weight basis or on an organic matter basis were not significantly different between the two lake types (Tables 6 and 7). On a per gram dry weight basis, the manganese content of meromictic lakes ranged from 0.21 to 1.88 mg/g dry weight as compared with a range of 0.35 to 0.99 mg/g dry weight in holomictic lakes. Similar results (no significant difference between meromictic and holomictic lakes) were obtained with the profundal sediments and the littoral to profundal ratio. In meromictic lakes, the littoral to profundal ratio ranged from 0.62 to 3.67 and from 0.54 to 1.88 in holomictic lakes. A ratio greater than one indicates that the profundal sediments contained less manganese than the littoral sediments.

6. Iron to Manganese Ratio

The littoral Fe:Mn ratio was significantly lower ($p = 0.005$) in meromictic lakes than in holomictic lakes (Table 8). Meromictic ratios varied from a low of 3.49 to a high of 24.62 as compared to a low of 30.86 and a high of 74.9 in holomictic lakes. In contrast, neither the Fe:Mn ratio in profundal sediments ($p = 0.057$), nor the relative change of this ratio between profundal and littoral sediments ($p = 0.057$) were significantly different between the two lake types, although probabilities did approach significant levels.

7. Chironomid Headcapsules

The number of chironomid headcapsules present in littoral and profundal sediments was expressed as both the number per gram dry weight

Table 6. Manganese Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Manganese Content as mg/g Dry Weight	Profundal Manganese Content as mg/g Dry Weight	Littoral/Profundal Manganese Ratio
Little Round	0.75	1.00	0.74
Pinks	1.88	0.51	3.67
Crawford	0.21	0.23	0.91
McGinnis	0.21	0.34	0.62
St. George-1	0.35	0.66	0.54
St. George-2	0.36	0.50	0.71
Coon	0.71	1.30	0.54
Found	0.96	0.56	1.71
White Duck	0.99	0.53	1.88
Canoe	0.75	0.70	1.07
U Value	9	6	10
Significance*	NS	NS	NS

* NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

Table 7. Manganese Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes.

Lake	Littoral Manganese Content as mg/g Organic Matter	Profundal Manganese Content as mg/g Organic Matter	Littoral/Profundal Manganese Ratio
Little Round	2.39	2.76	0.87
Pinks	29.89	1.09	27.42
Crawford	1.99	0.73	2.73
McGinnis	13.47	2.54	5.30
St. George-1	1.69	2.17	0.78
St. George-2	1.22	1.55	0.79
Coon	1.61	2.69	0.60
Found	12.63	1.26	10.02
White Duck	5.17	1.21	4.27
Canoe	12.02	2.06	5.83
U. Value	6	11	8
Significance*	NS	NS	NS

* NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

Table 8. The Iron to Manganese Ratio for the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Fe:Mn Ratio	Profundal Fe:Mn Ratio	Littoral/Profundal Fe:Mn Ratio
Little Round	24.6	25.9	0.95
Pinks	3.5	36.4	0.10
Crawford	10.3	34.6	0.30
McGinnis	4.1	13.9	0.29
St. George-1	33.7	34.0	0.99
St. George-2	37.4	66.4	0.56
Coon	42.6	29.3	1.46
Found	37.1	65.0	0.57
White Duck	30.9	45.1	0.68
Canoe	74.8	112.4	0.67
U Value	0	4	4
Significance*	S	NS	NS

* S: Significant difference ($p \leq 0.05$) existed between meromictic and holomictic lakes.

NS: No significant difference ($p > 0.05$) existed between meromictic and holomictic lakes.

of sediment and as the number per gram of organic matter (Tables 9 and 10). There were no significant differences between the ten meromictic and holomictic lakes studied with respect to their number of headcapsules present in littoral and profundal cores. A significant difference was approached ($p = 0.057$), however, among profundal cores between the two lake types when measured on a dry weight basis (Table 9). In meromictic lakes, the number of chironomid headcapsules ranged from 0.4 to 48 per gram dry weight of profundal sediment and between 28 and 234 per gram dry weight of sediment in holomictic lakes.

In comparing the relative change in headcapsules between the littoral and profundal zone of the same lake (littoral to profundal ratio), there was no significant difference between holomictic and meromictic lakes.

8. Chlorophyll SPDU

Chlorophyll did not significantly differ between the littoral sediments of meromictic and holomictic lakes (Table 11). In meromictic lakes, it ranged between 43.4 (Little Round) and 9.38 units per g organic matter (Pinks) with a mean of 64.9 (std. dev. 23.1). In holomictic lakes, chlorophyll degradation products ranged from 57.0 to 125.9 units in Coon Lake and St. George-2, respectively, with a mean of 50.3 (std. dev. 47.9). One unit represents an absorbance of 1 at 667 nm in a 10 mm cell when dissolved in 10 ml of solvent (Vallentyne 1955).

The profundal sediments of the meromictic lakes studied were not significantly different from the holomictic lakes, with respect to their chlorophyll content. In meromictic lakes chlorophyll varied from 87.5

Table 9. Chironomid Headcapsules in the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Chironomid Headcapsules as Number/gram Dry Weight	Profundal Chironomid Headcapsules as Number/gram Dry Weight	Littoral/Profundal Ratio
Little Round	15	38	0.41
Pinks	3	58	0.06
Crawford	54	24	3.12
McGinnis	1	0.4	2.50
St. George-1	75	106	0.70
St. George-2	79	79	0.97
Coon	19	28	0.69
Found	1	94	0.01
White Duck	120	234	0.51
Canoe	8	33	0.25
U Value	6.5	4	9
Significance*	NS	NS	NS

* NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

Table 10. Chironomid Headcapsules in the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Chironomid Headcapsules as Number/gram Organic Matter	Profundal Chironomid Headcapsules as Number/gram Organic Matter	Littoral/Profundal Ratio
Little Round	45	80	0.56
Pinks	50	123	0.41
Crawford	514	75	3.12
McGinnis	5	3	2.50
St. George-1	297	346	0.86
St. George-2	416	469	0.89
Coon	42	58	0.72
Found	11	61	0.18
White Duck	312	549	0.57
Canoe	132	98	1.35
U Value	10	10	10
Significance*	NS	NS	NS

* NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

Table 11. Chlorophyll Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Chlorophyll Content as SPD Units/g Organic Weight	Profundal Chlorophyll Content as SPD Units/g Organic Weight	Littoral/Profundal Chlorophyll Ratio
Little Round	43.4	189.9	0.23
Pinks	93.8	259.7	0.36
Crawford	73.0	429.5	0.17
McGinnis	49.5	87.5	0.57
St. George-1	99.2	173.1	0.57
St. George-2	125.9	178.2	0.71
Coon	62.3	138.7	0.45
Found	68.0	162.1	0.42
White Duck	72.4	138.4	0.52
Canoe	57.0	102.7	0.56
U Value	8	6	4.5
Significance*	NS	NS	NS

* NS: No significant difference ($p > 0.05$) existed between meromictic and holomictic lakes.

to 429.5 units per g organic matter as compared with a range of 72.5 (102.7 to 178.2 units per g organic matter) in holomictic lakes.

The relative change in chlorophyll and its degradation products between the littoral and profundal sediments (littoral/profundal ratio) of meromictic lakes was not significantly different from the littoral to profundal chlorophyll ratio in holomictic lakes. The littoral/profundal ratio ranged between 0.17 and 0.57 in meromictic lakes as compared to a low of 0.42 and a high of 0.94 in holomictic lakes.

9. Carotenoid SPDU

In the littoral sediments no significant difference existed between holomictic and meromictic lakes with respect to their carotenoid units (Table 12). One unit represents an absorbance of 1 at 450 nm in a 10 mm cell when dissolved in 10 ml of solvent.

The profundal carotenoid units in meromictic lakes were significantly higher than those in holomictic lakes. In the former, they ranged from 688.6 (Little Round) to 1522.9 (Crawford) with a mean of 1038.9 (std. dev. 379.8). In holomictic lakes, they ranged from 233.2 (White Duck) to 776.5 (St. George-2) with a mean of 190 (std. dev. 107).

In comparing the relative quantities of carotenoid pigment present in the littoral sediments with respect to that in the profundal sediments of the same lake, meromictic lakes exhibited a significantly lower littoral/profundal ratio. This indicated that meromictic lakes had consistently higher carotenoid pigments in the profundal sediments relative to the littoral sediments than did holomictic lakes.

Table 12. Carotenoid Content of the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Carotenoid Content as SPD Units/g Organic Weight	Profundal Carotenoid Content as SPD Units/g Organic Weight	Littoral/Profundal Carotenoid Ratio
Little Round	113.2	688.6	0.16
Pinks	255.0	1154.8	0.22
Crawford	245.0	1522.9	0.16
McGinnis	160.0	789.4	0.20
St. George-1	291.5	658.7	0.44
St. George-2	359.1	776.5	0.46
Coon	131.6	339.6	0.39
Found	119.1	474.9	0.25
White Duck	116.0	233.2	0.50
Canoe	123.2	261.9	0.47
U Value	12	0	0
Significance*	NS	S	S

* S: Significant difference ($p \leq 0.05$) between meromictic and holomictic lakes.

NS: No significant difference ($p > 0.05$) between meromictic and holomictic lakes.

10. Chlorophyll-Carotenoid Ratio

The relative amounts of chlorophyll and carotenoid units as depicted by the chlorophyll:carotenoid ratio did not differ significantly between the littoral sediments of meromictic and holomictic lakes (Table 13). In meromictic lakes, they ranged from 0.25 to 0.37 with a mean of 0.31 (std. dev. 0.05). In holomictic lakes, they ranged from 0.35 (St. George-1,2) to 0.64 (White Duck), with a mean of 48 (std. dev. 0.01). Similarly, no significant differences occurred in the profundal sediments. In meromictic lakes, a mean of 0.23 was found as compared with a mean of 0.37 in holomictic lakes.

Finally, the littoral/profundal, chlorophyll:carotenoid ratio did not significantly differ between meromictic and holomictic lakes. This indicates that between littoral and profundal cores there was no significant change in the relative abundance of either chlorophyll or carotenoids between the two lake types. In holomictic lakes, a mean of 1.33 (std. dev. 0.24) existed while in meromictic lakes a mean of 1.72 (std. dev. 0.76) was recorded (Tables 14 and 15).

11. Littoral Transects

Two approaches were utilized for the statistical analysis of the littoral sediment data in this study. In Tables 2 to 13, the littoral values represent the average of all of the littoral transects sampled within each lake. It is assumed that if a far larger number of cores had been collected, individually analyzed and averaged, then their average value would have been similar to the mean value used in this study. Using the mean littoral transect values, significant differences were

Table 13. Chlorophyll to Carotenoid Ratio for the Surface Sediments of Selected Meromictic and Holomictic Lakes

Lake	Littoral Chlorophyll/ Carotenoid Ratio	Profundal Chlorophyll/ Carotenoid Ratio	Littoral/Profundal Chlorophyll/ Carotenoid Ratio
Little Round	0.25	0.28	1.39
Pinks	0.37	0.23	1.64
Crawford	0.30	0.28	1.06
McGinnis	0.31	0.11	2.80
St. George-1	0.35	0.26	1.34
St. George-2	0.35	0.23	1.53
Coon	0.46	0.41	1.12
Found	0.58	0.34	1.69
White Duck	0.64	0.59	1.08
Canoe	0.47	0.39	1.20
U Value	4	4.5	9
Significance*	NS	NS	NS

* NS: No significant difference ($p > 0.05$) existed between meromictic and holomictic lakes.

Table 14. Within Lake Type Variation (Meromictic Lakes)

Analysis	N	Mean	Std. Dev.	C of V
Littoral				
Fe*	4	7.0	7.8	111.1
Mn*	4	0.8	0.8	103.9
Fe:Mn	4	10.6	9.8	92.7
Fe**	4	49.1	41.7	84.9
Mn**	4	11.9	13.1	109.7
O.M.*	4	14.3	11.2	78.6
Carb*	4	28.3	11.3	40.0
Chir**	4	153.5	241.2	157.1
Chir*	4	18.3	24.6	134.9
Chl**	4	64.9	23.1	35.6
Car**	4	193.3	68.3	35.3
Chl:Car	4	0.31	0.05	16.1
Profundal				
Fe*	4	14.3	9.7	68.1
Mn*	4	0.5	0.3	65.4
Fe:Mn	4	27.7	10.3	37.0
Fe**	4	39.1	12.0	30.8
Mn**	4	1.8	1.0	57.3
O.M.	4	34.7	15.9	45.9
Carb*	4	14.3	14.3	99.9
Chir**	4	70.3	49.7	70.8
Chir*	4	30.1	24.2	80.5
Chl**	4	241.6	143.8	59.5
Car**	4	1038.9	379.8	36.6
Chl:Car	4	0.23	0.08	34.8
Littoral/Profundal				
Fe*	4	0.4	0.2	52.5
Mn*	4	1.4	1.5	108.5
Fe:Mn	4	0.4	0.4	90.2
Fe**	4	1.2	1.0	79.5
Mn**	4	9.1	12.4	136.1
O.M.	4	0.5	0.3	60.0
Carb*	4	3.7	3.0	82.1
Chir**	4	2.4	3.0	123.4
Chir*	4	1.5	1.5	99.3
Chl**	4	0.3	0.2	55.6
Car**	4	0.2	0.03	15.8
Chl:Car	4	1.72	0.8	44.2

* relative to dry weight of sediment
** relative to organic weight of sediment

Table 15. Within Lake Type Variation (Holomictic Lakes)

Analysis	N	Mean	Std. Dev.	C of V
Littoral				
Fe*	6	29.2	16.3	57.8
Mn*	6	0.7	0.3	40.6
Fe:Mn	6	42.7	16.2	37.9
Fe**	6	281.9	343.4	121.8
Mn**	6	5.7	5.3	92.8
O.M.*	6	21.2	14.1	64.9
Carb*	6	8.2	10.7	130.4
Chir**	6	201.7	163.7	81.2
Chir*	6	50.3	47.9	95.3
Chl**	6	80.8	26.5	32.8
Car**	6	190.0	107.0	56.3
Chl:Car	6	0.5	0.01	25.0
Profundal				
Fe*	6	38.9	20.8	53.4
Mn*	6	0.7	0.3	42.3
Fe:Mn	6	58.7	30.5	51.9
Fe**	6	104.2	65.2	62.5
Mn**	6	1.8	0.6	31.9
O.M.*	6	38.9	7.6	19.6
Carb*	6	4.9	3.1	62.7
Chir**	6	263.5	219.6	83.4
Chir*	6	245.7	379.9	154.6
Chl**	6	148.9	28.2	18.9
Car**	6	457.5	221.4	48.4
Chl:Car	6	0.37	0.13	35.1
Littoral/Profundal				
Fe*	6	0.8	0.3	40.3
Mn*	6	1.1	0.6	56.0
Fe:Mn	6	0.8	0.4	42.7
Fe**	6	2.4	2.1	87.1
Mn**	6	3.7	3.8	101.6
O.M.*	6	0.6	0.3	61.8
Carb*	6	2.4	2.8	117.7
Chir**	6	0.8	0.4	51.3
Chir*	6	0.5	0.4	67.3
Chl**	6	0.6	0.2	28.8
Car**	6	0.4	0.1	21.4
Chl:Car	6	1.3	0.2	18.1

* Relative to dry weight of sediment

** Relative to organic weight of sediment found to exist between the littoral sediments of meromictic and holomictic lakes with respect to their carbonate, iron and iron to manganese ratio.

The technique adopted in this study did not recognize differences between transects in each of the lakes. To overcome this, all transects within a lake, rather than their average, were utilized in comparing differences between lake types (Tables 16 and 17). When each individual transect was used as a data point, rather than their average per lake, significant differences were found with respect to the chlorophyll to carotenoid ratio and manganese content of the littoral sediments (Tables 16 and 17). The mean standard deviation and coefficient of variation are shown in Table 18. The above transect by transect analyses indicated that by amalgamating transects within a lake, valuable information for between lake comparisons was lost.

Table 16. Organic Matter, Carbonate, Iron, Manganese and Iron to Manganese Ratio of the Littoral Transects of Selected Meromictic and Holomictic Lakes

Lake	Organic Matter (%)	Carbonate (%)	Iron mg Fe/g Dry Weight	Manganese mg Mn/g Dry Weight	Iron:Manganese Ratio
Crawford	9.59	38.05	1.69	0.22	7.5
	12.06	26.52	2.18	0.18	11.9
	10.03	37.44	2.46	0.22	11.4
Pinks	6.29	28.08	6.53	1.88	3.5
McGinnis	5.59	39.56	0.87	0.24	3.7
	5.04	32.04	0.72	0.22	3.3
	17.21	40.67	2.15	0.16	13.2
Little Round	38.18	11.96	15.46	0.73	21.2
	25.68	12.92	20.98	0.75	28.1
St. George-1	27.68	20.31	12.29	0.33	31.8
	9.18	34.28	10.42	0.38	35.3
	25.23	21.23	13.42	0.36	34.11
St. George-2	24.90	18.32	13.33	0.38	34.9
	33.90	17.26	13.42	0.34	39.9
Coon	46.31	3.59	29.40	0.56	52.2
	44.93	3.00	20.94	0.83	25.3
	40.87	3.77	33.93	0.68	50.0
Found	4.58	3.54	34.11	1.09	30.9
	10.61	0.66	35.97	0.83	43.7
White Duck	19.07	1.30	27.70	1.03	25.7
	8.91	0.74	36.88	1.05	36.0
	29.51	1.50	26.11	0.84	31.0
Canoe	9.41	0.92	38.75	0.60	64.3
	6.26	1.01	74.46	0.79	95.0
	3.05	0.49	56.22	0.88	65.1
U Value	56	12	6	32	2
Significance*	NS	S	S	S	S

Table 17. Chironomid Headcapsules, Chlorophyll, Carotenoids and Chlorophyll to Carotenoid Ratio of Littoral Transects of Selected Meromictic and Holomictic Lakes

Lake	Chironomid Headcapsules Number/g Organic Matter	Chlorophyll SPDU/g Organic Matter	Carotenoids SPDU/g Organic Matter	Chlorophyll: Carotenoid Ratio
Crawford	665	75.1	235.5	0.32
	459	77.0	278.7	0.28
	418	67.0	222.1	0.30
Pinks	50	93.8	254.1	0.37
McGinnis	0	56.6	194.2	0.29
	0	57.8	183.1	0.32
	16	34.2	102.3	0.33
Little Round	72	97.0	126.7	0.37
	18	39.8	99.8	0.40
St. George-1	360	86.7	241.5	0.36
	54	63.8	167.4	0.38
	476	146.9	465.7	0.32
St. George-2	442	110.9	361.5	0.31
	391	140.8	356.7	0.40
Coon	61	33.5	74.1	0.45
	53	40.8	99.2	0.41
	11	112.6	221.5	0.51
Found	1	73.8	112.2	0.66
	21	62.2	126.0	0.49
White Duck	389	72.1	100.5	0.72
	0	103.8	182.7	0.57
	547	41.2	64.9	0.64
Canoe	111	61.9	155.8	0.40
	182	53.0	104.2	0.51
	104	56.1	109.7	0.51
U Value	61	54	64	17.5
Significance*	NS	NS	NS	S

Table 18. Littoral Core Variation Within Holomictic and Meromictic Lakes

Analysis	N	Mean	Standard Deviation	Coefficient of Variation
<u>Meromictic Lakes</u>				
Fe*	9	5.89	7.32	124.28
Mn*	9	0.51	0.56	109.80
Fe:Mn	9	11.51	8.52	74.02
Chironomid**	9	188.60	253.88	134.60
Chlorophyll**	9	66.47	21.75	32.73
Carotenoids**	9	186.65	66.20	35.48
Chl:Car	9	0.33	0.04	12.08
Organic Matter*	9	14.41	11.06	76.75
Carbonates*	9	30.80	11.11	36.07
<u>Holomictic Lakes</u>				
Fe*	16	29.82	17.30	58.01
Mn*	16	0.68	0.27	39.71
Fe:Mn	16	43.44	18.40	42.36
Chironomid**	16	200.16	196.67	98.26
Chlorophyll**	16	78.77	34.92	63.90
Carotenoids**	16	183.97	117.56	25.63
Chl:Car	16	0.48	0.12	68.46
Organic Matter*	16	21.53	14.74	68.46
Carbonates*	16	8.06	10.57	131.14

* Relative to dry weight of the surface littoral sediments.

** Relative to the organic weight of the surface littoral sediments.

B. CRAWFORD LAKE CORE

1. Organic Matter, Carbonate and Mineral Content

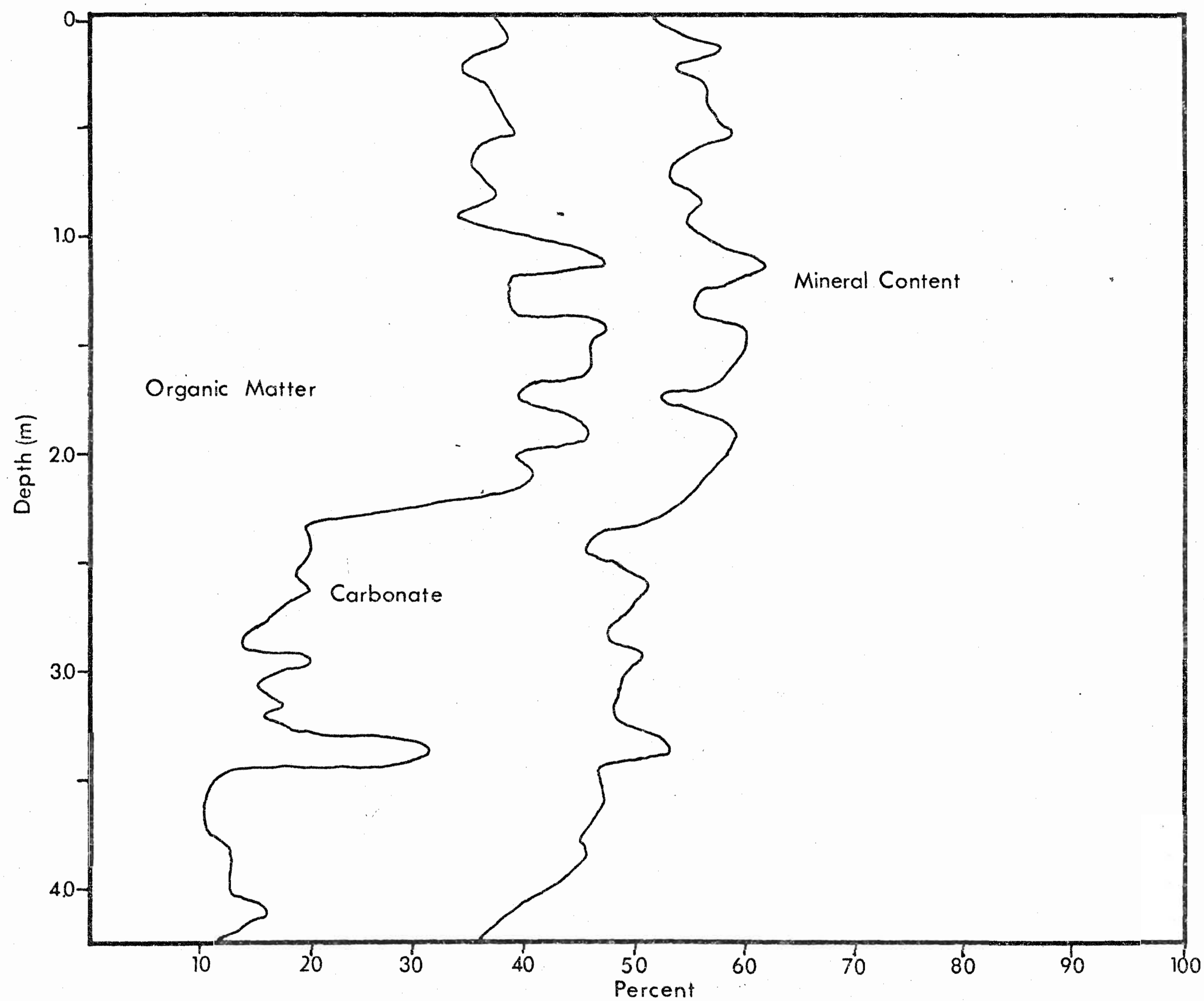
Vertical variations in organic matter, carbonate and mineral content of the Crawford Lake profundal core was plotted as a function of the dry weight of the sediments at each depth (Figure 12). Organic matter and carbonates displayed the largest vertical variation while the mineral (non-organic, non-carbonaceous material) content remained relatively constant.

The major increases in organic carbon reflect the development of terrestrial vegetation and increases in autochthonous biomass. The deepest (oldest) portion of the core (420-425 cm) represents a period of low organic production (percent organic matter = 9.2), which was deposited during a period when clay and silt accumulated on the lake bottom. This latter fraction accounted for approximately 70% of the dry weight of the sediment at that depth.

Between 425 and 230 cm, the percentage of organic matter in the core was relatively low (9-14%) with the exception of a large peak (30%) at a depth of 335 cm. During the same period, carbonates were relatively high, varying from 19 to 36%. This pattern (low organic matter and high carbonate content), was reversed in the upper 200 cm where organic matter fluctuated between 32 and 46% of the dry weight of the sediment, while carbonate ranged between 13 and 19%.

During the early development of Crawford Lake, the mineral content comprised the largest proportion of the sediment varying from a low of 40% to a high of 71%.

Figure 12. A depth profile indicating the percentage organic matter, carbonate and mineral content in Crawford Lake core.


Mineral Content
Organic Matter
Carbonate
Depth (m)
0
1.0
2.0
3.0
4.0
10
20
30
40
50
60
70
80
90
100
Percent

2. Chironomid Headcapsules

Vertical variation in the number of chironomid headcapsules deposited in the profundal sediments of Crawford Lake were expressed relative to the dry weight and organic matter content of the sediments (Fig. 13). In the bottom of the core (425-430 cm), relatively few headcapsules were present (approximately 3 per gram organic matter). This represented the lowest density attained throughout the lakes' ontogeny. Sixty-three headcapsules per gram organic matter were recovered at a depth of 35 cm which represented the greatest density attained in the core. Between these two depths, the number of headcapsules underwent periods of both increasing and decreasing densities (Fig. 13). The trends exhibited by fossil chironomid headcapsules were significantly correlated with the trends in percent organic matter and chlorophyll pigment concentrations (Table 19).

3. Chlorophyll and Carotenoid SPDU

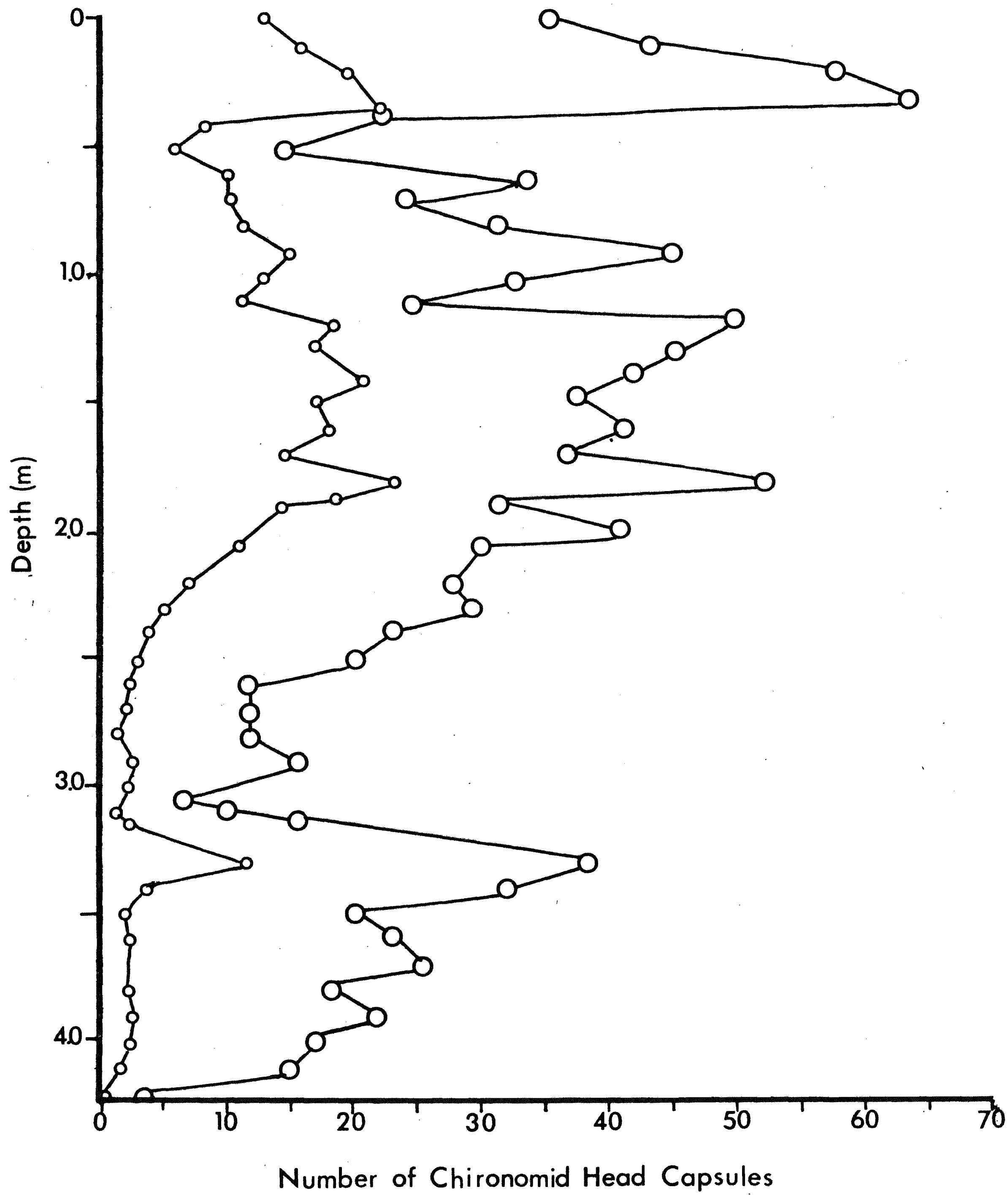
Sediment deposited at a depth of 425 to 275 cm were characterized by relatively low pigment concentrations with the exception of two peaks occurring at 400 and 335 cm (Fig. 14). Changes in the amplitude of the carotenoid peaks were more distinct than those exhibited by chlorophyll, although their relative increase was similar. For example, carotenoid peak at 400 cm represented a 5.8 fold increase from its pre-peak low as compared with a 5.0 fold increase in chlorophyll. Generally, any change in the abundance of pigments deposited and preserved in the sediments is best reflected by the variation in the carotenoids.

The period from 275 to 110 cm was characterized by an increasing trend in both chlorophyll and carotenoid concentrations with some interim

Figure 13: A depth profile indicating the number of fossil chironomid headcapsules per gram dry weight ( )

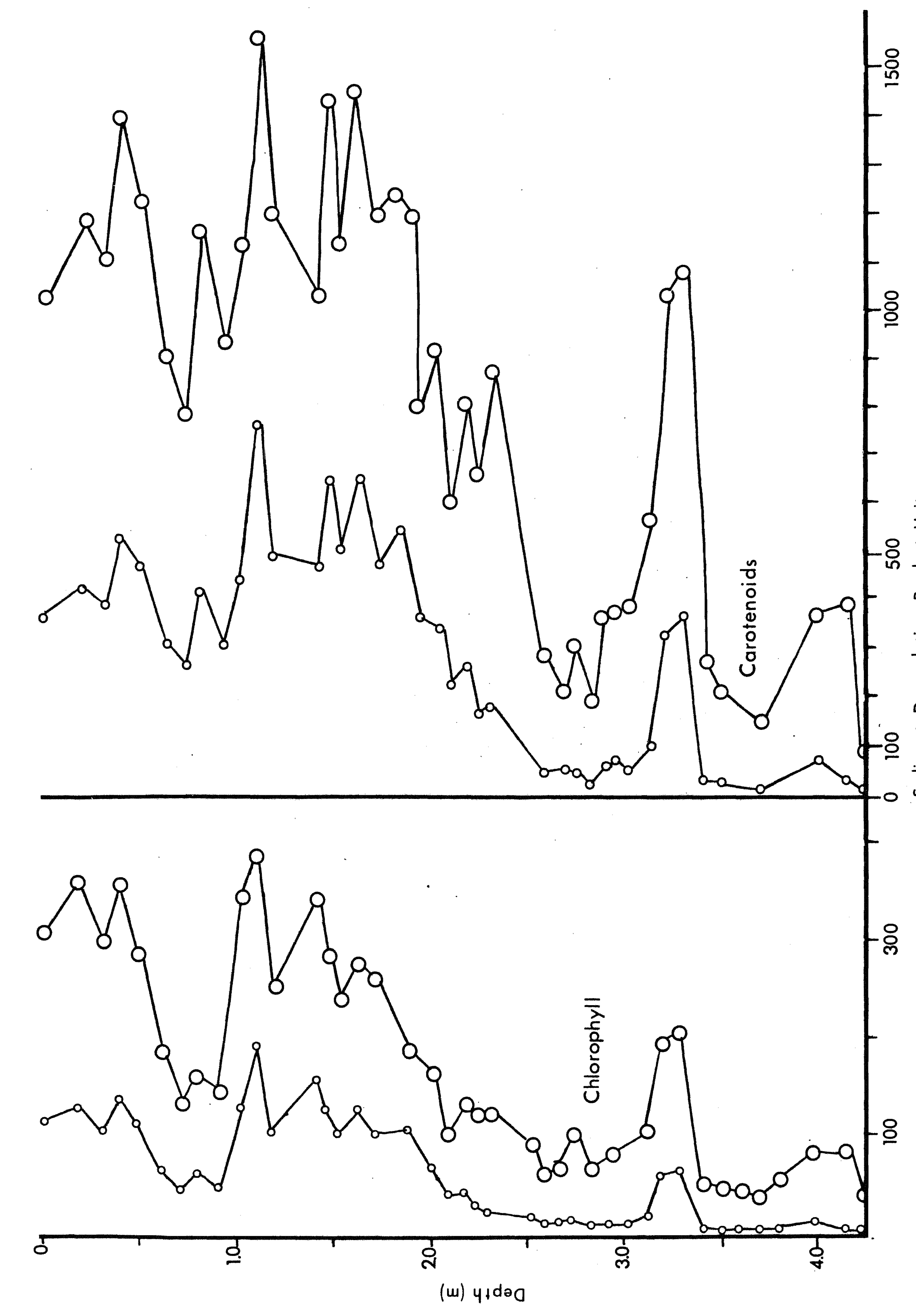
per gram organic weight ( )

of sediment in Crawford Lake core.



0
1.0
2.0
3.0
4.0
Depth (m)
0
10
20
30
40
50
60
70
Number of Chironomid Head Capsules

Figure 14. Vertical distribution of chlorophyll and carotenoids per gram dry weight (o—o—o—o—o—o) and per gram organic weight (O——O——O) in Crawford Lake core.


Chlorophyll
Carotenoids
Sediment Degradation Product Units
Depth (m)
0
100
300
500
1000
1500
1.0
2.0
3.0
4.0

fluctuation. During this phase of the lake's history, chlorophyll SPDU increased from 17 to 191 units as compared with an increased from 51 to 776 units for carotenoids over the same period (i.e., 275-110 cm).

The temporal changes in the top 100 cm were characterized by comparatively large flucturations in both chlorophyll and carotenoids though relative to changes which have taken place in the core they were comparatively small. In the upper twenty centimetres of the sediment core, both pigments steadily decreased in concentration.

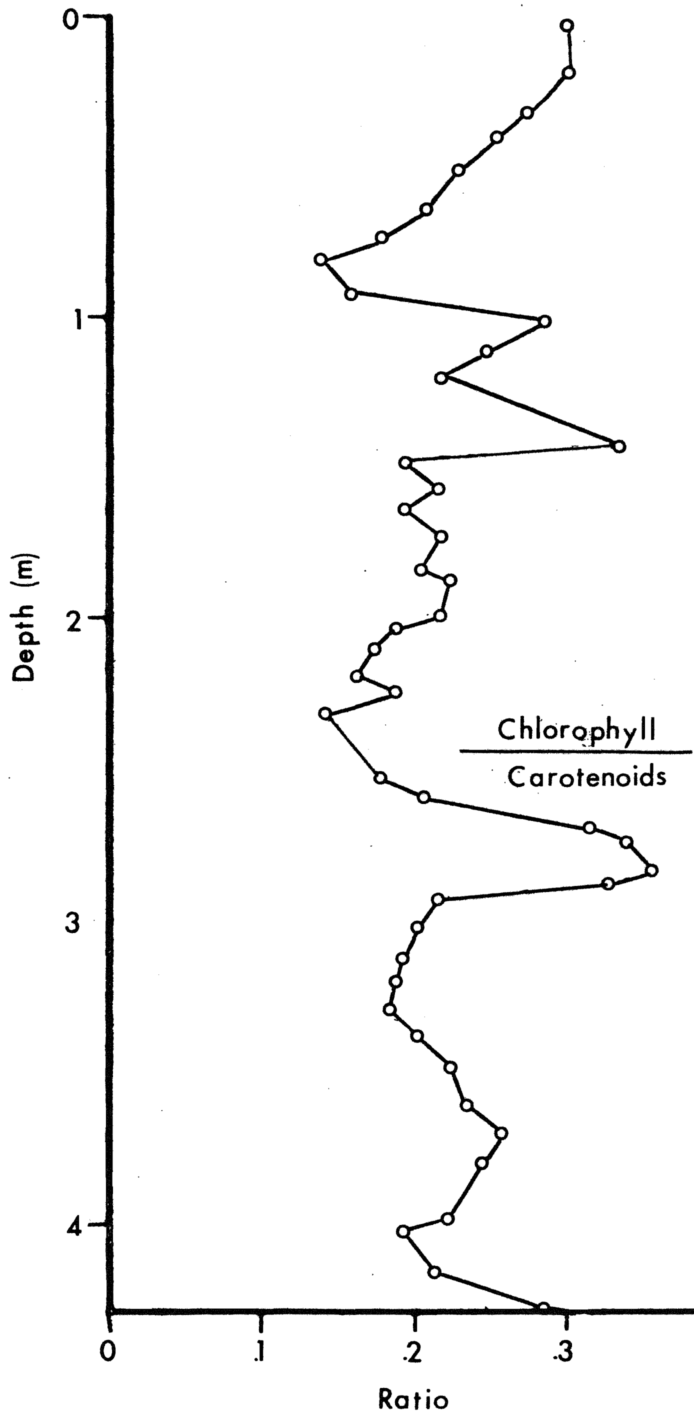
4. Chlorophyll to Carotenoid Ratio

The chlorophyll to carotenoid ratio reflects the relative abundance of chlorophyll with respect to the number of carotenoid units present in the sediments. In the Crawford Lake core, chlorophyll and carotenoids exhibited similar trends though the relative amounts of each underwent considerable flucturations, as indicated by their ratio (Fig. 15).

At the bottom of the core (425 cm) the chlorophyll to carotenoid ratio was high (0.35). This depth represents the period shortly after the lake's formation. The ratio then declined to 0.20 at 410 cm as a result of increases in the carotenoid content of the sediments (Fig. 14). Between 410 and 80 cm, the ratio underwent numerous fluctuations (Fig. 15), although no apparent increases or decreases in these trends were exhibited. The observed peaks in the ratio during this period were largely a result of rapid decreases in the carotenoid content of the sediments.

Lastly, from 80 cm to the surface of the core, the chlorophyll to carotenoid ratio underwent a steady increase from 0.14 to 0.31. However, unlike the previous peaks, this occurred during a period when the carotenoid sediment concentrations was quite variable.

Figure 15. Depth profile of the chlorophyll to carotenoid ratio in the Crawford Lake core.



0
1
2
3
4
Depth (m)
Chlorophyll
Carotenoids
0
.1
.2
.3
.4
Ratio

5. Iron

Temporal change in the iron content of the profundal sediments of Crawford Lake was plotted (Fig. 16). The iron stratigraphy resembled the mineral stratigraphy and hence may reflect its primary source of origin. In comparison with changes exhibited by other variables such as organic matter and pigments, iron remained relatively constant during the lake's development.

Between 430 and 340 cm, iron underwent its greatest temporal change, decreasing from 21.0 to 6.6 mg Fe per g dry weight, with a sharp peak at 405 cm. This latter peak coincided with peaks observed in organic matter and pigment stratigraphy. The upper 340 cm of the core remained relatively constant.

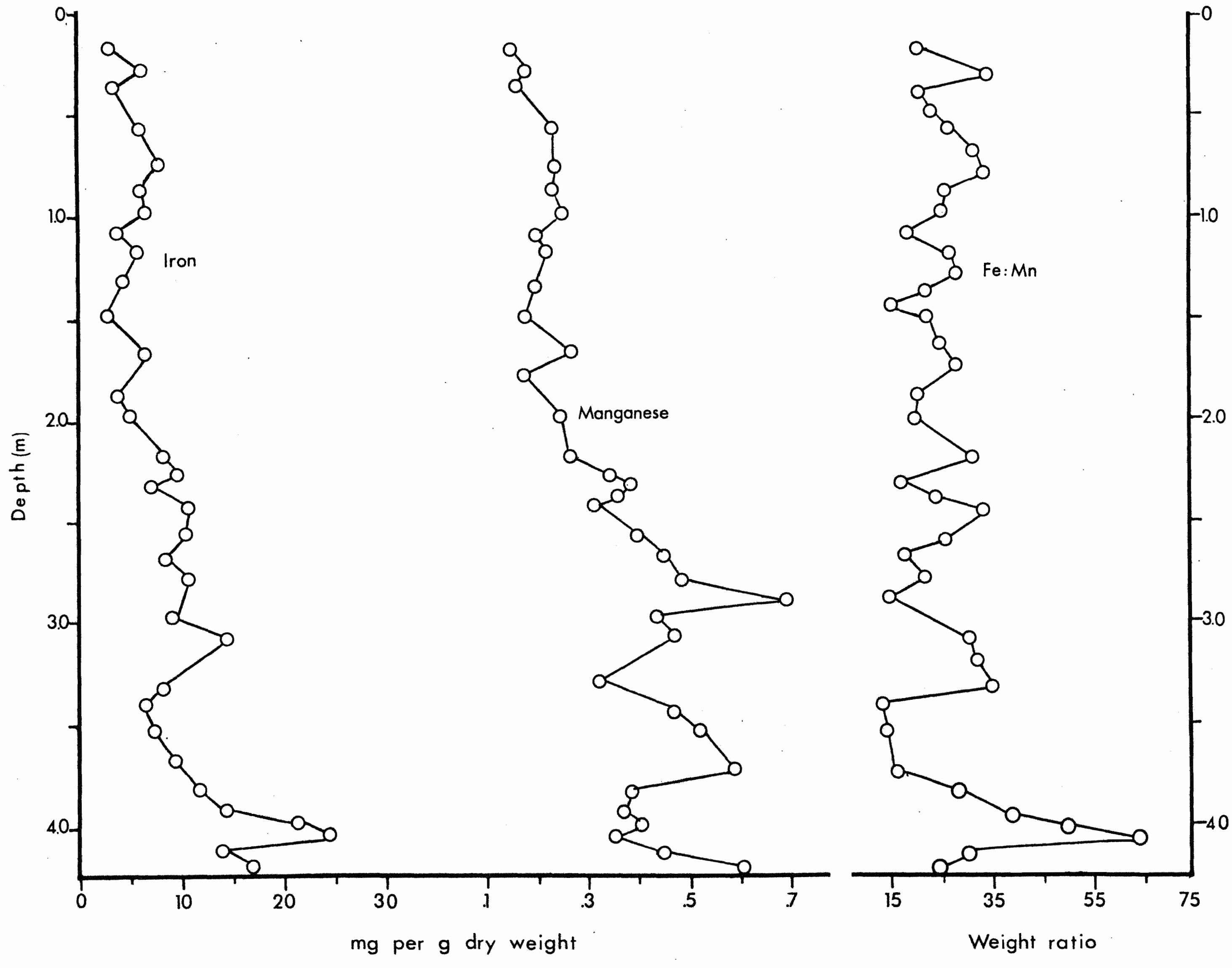
6. Manganese

Changes in the manganese content of the sediment with respect to time are shown in Figure 16. The manganese stratigraphy may be divided into two zones relative to its changes in comparison with those exhibited by iron. The first zone extended from 430 to 290 cm. This represented a period when manganese often varied indirectly with iron. The second zone (290 to 0 cm) was characterized by similar directional changes between the two elements. Temporal changes in manganese as with those in iron, resembled temporal changes in the clastic content of the sediment.

7. Iron to Manganese Ratio

Changes in the iron to manganese ratio during the development of Crawford Lake reflected two distinct zones (Fig. 16). Zone one (425 to

Figure 16. Vertical distribution of Iron (mg Fe/g dry weight), Manganese (mg Mn/g dry weight) and Iron:Manganese Ratio (weight ratio)


Depth (m)
0
1.0
2.0
3.0
4.0
Iron
Manganese
Fe:Mn
0
10
20
30
.1
.3
.5
.7
15
35
55
75
mg per g dry weight
Weight ratio

350 cm) exhibited a decreasing trend with one distinctive peak occurring at 405 cm. In contrast, zone two (355 to 0 cm) tended towards a relatively constant ratio as opposed to one that either increased or decreased. Furthermore, in zone two, although the ratio underwent a great number of fluctuations, their magnitude was much less than that observed in zone one. In zone two, the iron to manganese ratio was 13.5 at 355 cm and 20.6 near the surface. During the interim, it was quite variable fluctuating between a low of 13.5 and a high of 35.6, in response to changes in both the iron and manganese concentrations.

8. Regression Analysis

The correlation coefficients of each variable regressed against all others is provided in Table 19. Its sole purpose is to provide a quantitative measure of the somewhat obvious relationships that exist between variables along the Crawford lake profundal core.

Table 19. Coefficient of Correlation matrix for 9 variables in the Crawford Lake core.

	2	3	4	5	6	7	8	9
1	0.964*	0.019	0.783*	0.872*	0.781*	0.649	0.811*	0.299
2		0.170	0.561	0.910*	0.730*	0.670*	0.831*	0.293
3			0.130	0.177	0.088	0.217	0.144	0.131
4				0.809*	0.800*	0.644	0.820*	0.229
5					0.891*	0.699*	0.907*	0.267
6						0.362	0.814*	0.095
7							0.536	0.828*
8								0.009

1--chlorophyll
2--carotenoids
3--chlorophyll to carotenoid ratio
4--chironomid headcapusles
5--organic matter
6--carbonate
7--iron
8--manganese
9--iron to manganese ratio

* Significant at p = 0.05

IV. DISCUSSION

This study was undertaken to determine whether the onset of meromixis (which results in a permanently anaerobic monimolimnion) would have sufficient impact on the physical, chemical and biological characteristics of a previously holomictic lake to significantly change the sedimentary record of that lake.

Short cores were collected from the profundal and littoral zones of four meromictic and six holomictic lakes. In addition, a single long core was taken from the profundal zone of meromictic Crawford Lake, Ontario. The thesis discussion is therefore divided into four parts:

A. a discussion of the short core analyses from the littoral zone of each lake,

B. a discussion of the surface sediments (short cores) from the profundal zones of each lake,

C. a critique of the surface sediment study, and

D. an analysis of the long core.

Sediment chemistry, sediment pigments and fossil chironomid head-capsules are compared for holomictic and meromictic lakes and, for temporal changes within a known meromictic lake.

A. LITTORAL ZONE

Two to three transects were taken in the littoral zone of each of ten lakes. Three or four short cores were taken along each of these transects and combined to form a composite sample for each transect. Combining cores along all of the transects into one composite sample for each of the four transects was felt necessary in order to maintain the number of samples within a manageable size.

To date, no multiple factor comparative study had ever been undertaken in which potential sediment differences between holomictic and meromictic lakes were investigated.

1. Chemistry

(a) Organic Matter and Carbonate Concentrations

The organic matter content of the littoral sediments (relative to the dry weight of the sediment) did not statistically differ between the meromictic and holomictic lakes utilized in this study. However, three of the four meromictic lakes exhibited significantly higher carbonate concentrations in their littoral sediments than those of the six holomictic lakes (Table 3). This was largely a consequence of their geographical location. The three meromictic lakes whose littoral sediments were carbonate-rich were not located on the Canadian Shield. If carbonates were deposited in the littoral sediments at a high rate relative to other material, then this in turn would have a diluting effect on other substances as they accumulated in the sediments (i.e., organic matter, silt, etc.) per unit volume of sediment. The importance of this will become more obvious in the following section.

(b) Iron

The littoral sediments of the meromictic and holomictic lakes studied differed significantly with respect to their iron concentration (Tables 4 and 16). The data suggest that this is not a consequence of meromixis but simply a result of differences in the physical composition of the sediment. Presumably, the high amounts of carbonate have had a diluting effect on the iron-containing material.

In support of this, Bortleson (1971) in a study of several Wisconsin lakes (none of which were meromictic) found that the concentrations of iron in noncalcareous lakes were higher than the calcareous lakes, though the deposition rates of both iron and manganese were higher in calcareous lakes. Mackereth (1966) and Bortleson (1971) state than an iron supply is associated with increased surface runoff. Carroll (1958) also found that the association of iron with clay minerals is an important means whereby iron is transported by rivers to lakes. In this study, the non-organic, non-carbonaceous material (termed mineral content) did not differ significantly between the two lake types (*i.e.*, holomictic *vs* meromictic) and hence the carbonate material has had a diluting effect on the iron in meromictic littoral sediments.

(c) Manganese

When the mean littoral manganese concentrations were compared, no significant differences were found although Mann-Whitney "U" test values approached significance. Differences due to the diluting effect of carbonate as occurred with iron were not apparent. In this respect, it is possible that preferential leaching of manganese from the watershed occurs and thus differences induced by sediment differences were obscured. If this was the case, then it follows that relatively more manganese is entering the littoral sediments of meromictic lakes than holomictic lakes (per unit volume of sediment) in order to compensate for the diluting effect of carbonates.

As explained in the methods section of this thesis, the littoral zone transects were averaged to give a single pooled littoral zone value for each lake. The expansion of the sample size, which the use of transect data permitted, allowed the demonstration of significant differences which could not have been demonstrated from the pooled data alone. For example, there was no significant difference in manganese concentrations between the littoral zone sediments of holomictic and meromictic lakes when the pooled transect data were used ($p > 0.1$). However, when individual transect values were used, a significant difference was established ($p < 0.05$). The sample sizes for the holomictic and meromictic lakes using the pooled data were 6 and 4, respectively. Using the non-pooled transect data, the sample sizes increased to 9 and 16 respectively. This increase in the apparent sample size, which was the result of using the individual transect data sets, permitted me to show significant differences in the manganese concentration between littoral zones of meromictic and holomictic lakes.

When chemical transport in the drainage system occurs by the reduction of the mobile manganous and ferrous forms, considerable separation of the two elements may be expected since manganese is more readily reduced than iron. Mackereth (1977) postulated that enrichment of manganese with respect to iron in Lake Windermere was brought about by the onset of reducing conditions in the soils of sufficient intensity to produce manganous ions but not intense enough to effect the large scale reduction of iron to ferrous ions. Thus manganese would have been preferentially removed from the drainage soils and carried (in solution) to the oxidized lake waters.

In this study, it was impossible to state whether differences in the manganese concentration between meromictic and holomictic lakes was a result of preferential leaching from the watershed or a result of diluting effects due to the nature of the sediments. What is important, however, is that neither apparent cause was a consequence of meromixis. This is substantiated by the fact that Little Round Lake, a non-calcareous meromictic lake exhibited concentrations within the range exhibited by the holomictic lakes sampled during this study.

(d) Iron to Manganese Ratio

The significantly lower iron to manganese ratio in the littoral sediments of meromictic lakes appears to be due to the significantly lower iron concentrations in meromictic littoral sediments. This conclusion is based on the fact that greater differences in the iron content of the sediment and much smaller differences in the manganese content were found between meromictic and holomictic lakes. Therefore, I believe that the nature of the littoral sediment rather than meromixis *per se*, has been instrumental in creating the observed statistical differences with respect to the iron to manganese ratio.

2. Fossil Chironomid Remains

No significant differences were detected between meromictic and holomictic lakes with respect to their total number of fossil chironomid remains in their littoral sediments. The littoral environment of meromictic and holomictic lakes does not appear to differ with respect to the type of habitat afforded these dipteran larvae. The influence of substrate (Erman 1973, McLachlan 1975), oxygen (Peter 1971, Brinkhurst 1974) and food (Provost and Branch 1957, Jonasson et al. 1967, Hynes 1970) have all been identified as important factors controlling their abundance and distribution.

It is interesting to note that within a particular lake, those sediments that contained the greatest amount of organic matter, generally contained the largest number of fossil chironomid headcapsules. However, this relationship was not maintained between lakes (Table 20). Presumably within a given lake this would reflect chironomid preference for an organically rich substrate, while between lakes other factors prove more important in regulating their absolute abundance.

The important point is that there was no significant difference between meromictic and holomictic lake littoral zone chironomid densities. This is to be expected as it is the lack of profundal oxygen that differentiates meromictic from holomictic lakes.

3. Pigments

In this study, no significant differences were detected between the two lake types with respect to their chlorophyll and carotenoid content of their littoral sediments.

The lack of significance observed was presumably a result of the variability exhibited within each group of lakes. I believe that this was a consequence of a number of different factors that may influence the concentration of fossil pigments in lake sediments. Invariably, those sediments containing relatively larger quantities of organic matter will contain greater amounts of fossil pigments. Furthermore, the organic

Table 20. Organic Matter content and Chironomid headcapsules present in the littoral transects of selected Meromictic and Holomictic lakes.

Lake	Organic Matter (%)	Chironomid Headcapsules per g of Organic Matter
Little Round	38.18	72
	25.68	18
McGinnis	5.59	0
	5.04	0
	17.21	5
Found	4.58	1
	10.61	21
White Duck	19.07	389
	8.91	0
	29.51	547

matter fraction of the sediment originates from both autochthonous and allochthonous sources. The amount of chlorophyll and carotenoid pigments in the sediments will vary depending on the source of the material (Gorham and Sanger 1972). Generally, allochthonous material contains greater quantities of chlorophyll relative to carotenoids than does autochthonous material. Therefore, any variable that influences the input of allochthonous material to a lake such as lake morphometry, size of the watershed or erosional intensity will in turn influence the relative amounts of chlorophyll and carotenoids in the sediment.

Because of the above influences, it was not possible to differentiate meromictic from non-meromictic lakes based on pigment differences in their littoral zone sediments. This is what one might expect to find since each variable was subjected to seasonally similar oxygen, temperature and light conditions. Consequently, in the littoral zone it would appear that the fossil pigments were relatively unaffected by the anaerobic conditions that prevailed in the profundal zone of the meromictic lakes. Although this may seem self-evident, it is a very important point. Its significance will become more apparent later in the discussion.

4. Summary

In summary, the littoral zone surface sediments significantly differed between meromictic and holomictic lakes with respect to their iron, manganese and carbonate content as well as their iron to manganese ratio. The observed differences were believed to be a consequence of the high carbonate content of three of the four meromictic lakes rather than a consequence of the process of meromixis itself.

B. PROFUNDAL ZONE SEDIMENTS

The basic underlying assumption of all paleolimnological studies is that changes in the profundal sediments reflect changes in the lake as a whole. The profundal zone sediment composition is a result of both direct autogenic and allogenic sedimentation plus secondary redeposition of sediment from the littoral zone through resuspension and slumping processes in the lake.

In meromictic lakes, anaerobic conditions prevail below the chemocline while in holomictic lakes anaerobic periods, if they occur at all, are confined to the hypolimnion during periods of thermal stratification. As discussed previously, the anaerobic monimolimnion of meromictic lakes influences the physical, chemical and biological variables contained within their sediments. Hence it is in the profundal sediments that the effects of meromixis should be most evident.

1. Chemistry

(a) Iron

The iron content of the profundal sediments of meromictic lakes was significantly lower than in holomictic lakes. Due to non-significant statistical differences of organic matter and carbonate between the two lake types, differences in the iron concentration cannot be accounted for by differences in sediment texture. In contrast, significantly higher carbonate concentrations in meromictic littoral sediments were used to explain their significantly lower littoral iron concentrations.

The lower iron content in the profundal sediments of meromictic lakes was somewhat surprising as Kjensmos' work (1968) on sediment cores suggests that an increase in the iron to manganese ratio occurs as a result of the sediment re-enrichment of iron relative to manganese. This results from both the reprecipitation of iron as FeS and the loss of manganese from the profundal sediments. His study, however, was concerned with temporal changes within the same lake. This study, in contrast, compares differences between lakes. Therefore, in theory, an increase in the iron content of the profundal sediments of the meromictic lakes studied may have occurred when meromixis was initiated. However, because my particular group of meromictic lakes generally contained less iron than my holomictic lakes, their expected higher profundal iron concentrations were not observed. Thus, differences within each lake type may obscure differences between lake types.

In order to evaluate such problems, the change between the littoral and profundal zones of each lake were determined, as represented by the littoral to profundal ratio of each parameter studies. For each lake, the ratio represented a comparison of an area of the lake that was never anaerobic (littoral zone) with an area that underwent varying lengths of anaerobic conditions (profundal zone). The assumption made was that the profundal sediments would reflect littoral zone changes. Consequently, if the littoral sediments contained large quantities of iron, this would be reflected in large quantities of iron being present in the lake's profundal sediments. This assumed relationship was only partially supported by the data. The sediment iron content supported the above rationale, but some discrepancies were exhibited by the fossil pigment data.

In theory, by comparing the littoral to profundal ratios, the quantitative differences between lakes should become less distinct. A lake with both low littoral and low profundal concentrations for a particular variable may not differ from a lake with high littoral and profundal concentrations, as the relative change (littoral to profundal ratio) may approximate each other. Using this procedure (littoral to profundal ratio comparisons), it was thought that excessive increases in the amount of a particular variable in the profundal sediments of meromictic lakes could be directly related to meromixis.

The littoral to profundal ratios were compared. Meromictic lakes as a group were found to exhibit significantly lower littoral to profundal iron ratios than did holomictic lakes. This indicates that meromictic lakes have more iron in their profundal sediments relative to that present in the littoral sediments than do holomictic lakes. It is suggested that this apparent iron enrichment is a consequence of meromixis, possibly due to the precipitation of iron as ferric sulphide (Dickman and Hartman 1979). Therefore, within a meromictic lake, one might expect to find an increase in the iron content of its profundal sediment during that period along a core when the lake underwent the transition from holomictic to meromictic status. This, however, is purely conjectural on my part and would require more intensive research. The relatively low iron concentration in the littoral sediments of meromictic lakes (due to the diluting effect of carbonates, for example) may have influenced the littoral to profundal ratio. In this respect, it is possible that age differences between littoral and profundal sediments were greater in meromictic lakes than in holomictic lakes. Hence the top 15 cm of littoral sediments in meromictic lakes represents relatively younger sediments than the same sediment volume from holomictic lakes.

(b) Manganese

The manganese content of the profundal sediments did not differ significantly between the two lake types. Thus, in this study, any changes in the manganese content of the profundal sediments that may have occurred as a consequence of meromixis were not evident. The variability between lakes within a group was sufficiently large to obscure any between group differences. Consequently, it was impossible to classify any of my lakes on the basis of their holomictic or meromictic status based on the manganese content of their profundal sediments.

The relative change in the iron to manganese ratio between the two zones (littoral and profundal) of each lake were compared utilizing the littoral to profundal ratio. Once again, no significant differences were obtained between holomictic and meromictic lakes. This is somewhat surprising as it is well documented that under anaerobic conditions manganese is mobilized from the sediments thus reducing its sediment concentration. Hence, one would expect less manganese in the profundal sediments of meromictic lakes relative to their littoral sediments, in comparison with holomictic lakes. In fact, five of the ten lakes studies (4 holomictic and only 1 meromictic) exhibited lower manganese concentrations in their profundal sediments than in their littoral sediments. The high manganese content in the littoral sediments of meromictic Pinks lake was probably due to mica mine tailings which are manganese rich (Hogarth 1970). Therefore, the presence of an anaerobic monimolimnion appeared to have had no appreciable effect on the manganese content of the profundal sediments. This may partially reflect the dilution effect of carbonates on the littoral meromictic sediments which may have created the potential age differences between zones of a lake. Little Round Lake, a non-calcareous meromictic lake, exhibited littoral and profundal manganese concentrations similar to holomictic lakes. Secondly, some holomictic lakes (Coon and St. George-2) periodically develop anaerobic hypolimnia. In such lakes, because manganese enters solution at a higher redox-potential than iron, manganese may be preferentially removed from the sediments. This in turn may create a diffusional gradient in which manganese moves from deeper to shallower depths of the sediment column. When these lakes circulate, the accumulation of manganese in the hypolimnetic waters may then be redeposited in the surface profundal sediments.

(c) Iron to Manganese Ratio

The onset of meromixis results in a reduction in the manganese content of the profundal sediments and a re-enrichment of iron, resulting in an increase in the iron to manganese ratio (Kjensmo 1968a, b). Hence, one might expect to find a larger iron to manganese ratio in the profundal sediments of meromictic lakes than that which occurs in holomictic lakes. This is assuming however that the anaerobic monimolimnion is the only factor that differs between the lakes. In this study marginally significant differences ($p > 0.1$) were found between meromictic and holomictic lakes with respect to their profundal iron to manganese ratios. The ratio was somewhat lower in meromictic profundal sediments. Consequently, though the iron to manganese ratio may have increased in each of the meromictic lakes when meromixis was initiated, there was no evidence that this ratio differed substantially from that found in holomictic lakes. However, it is possible that, although each lake type did not differ as a whole, each lake may have undergone subtle changes within itself when meromixis was initiated.

The littoral to profundal iron to manganese ratios were compared in order to determine whether there was a significant change between the littoral and profundal zones within the same lake. No significant differences were observed ($p < 0.05$) although marginal significance was attained ($p > 0.1$), with meromictic lakes tending towards a lower littoral to profundal ratio. This was a result of lower iron to manganese ratios in the littoral sediments of meromictic lakes relative to that present in the profundal sediments, rather than the reverse.

2. Fossil Chironomid Remains

In theory, the lack of oxygen which prevails in the monimolimnion of meromictic lakes should prevent the development of a profundal chironomid population. This is supported by the fact that in the meromictic Pinks Lake, no living chironomid fauna exists in the profundal sediments (Oliver and Danks 1975). Furthermore, according to Iovino (1975) the chironomid headcapsule remains in the sediments are indicative of the living chironomid population. Therefore, in meromictic lakes, I would have expected to find very few chironomid headcapsule remains in the profundal sediments, assuming that only a limited redeposition from the littoral sediment had occurred.

In this study, no significant differences were found between the fossil chironomid headcapsule densities in the profundal sediments of meromictic and holomictic lakes. This was in all likelihood due to extensive redeposition of their head capsules from the littoral zone. The evidence for this was based on the presence of numerous littoral zone diatoms which were resuspended and deposited in the profundal zone (J. Smol, pers. comm.). Redeposition in meromictic lakes is presumably largely a result of slumping rather than wind-induced resuspension, due to their characteristic steep sided basins. In holomictic lakes, redeposition is more likely to be the result of wind induced resuspension of littoral zone sediments. In theory, if little redeposition occurred in meromictic lakes, then a large littoral to profundal chironomid headcapsule density ratio would be expected.

When the littoral to profundal ratios between the two lake types were compared with respect to the total number of fossil chironomid headcapsule remains, no significant differences were observed. This suggests that there are no differences in the littoral transport of headcapsules to the profundal zone between holomictic and meromictic lakes. This assumes that equal densities occur in both parts of the lake. On the other hand, if one assumes that there are fewer headcapsules in the profundal sediments of meromictic lakes as a consequence of meromixis, then greater littoral to profundal transport must take place in order to provide the acquired results. Unfortunately, it is not possible to determine which assumption is valid from my data.

If total number of fossil chironomid headcapsule remains are to be a reliable technique for determining meromixis, then it is necessary to prove that their temporal changes in headcapsule densities reflect real changes in the profundal zone chironomid population. Hence, if there were no living chironomids in the profundal zone but their remains were transported there from the littoral zone, their remains would not reflect real changes in the profundal zone chironomid population unless it were possible to distinguish between littoral and profundal zone species. If the chironomid remains can be identified as littoral or profundal species, then it may be possible to express their number in the profundal sediments as profundal species only. Only in this way would fossil chironomid headcapsule densities prove to be a valuable paleo-indicator of the onset of meromixis.

3. Pigments

Lacustrine sediment fossil pigments may be indicative of lake trophic status (Gorham and Sanger 1974). More productive lakes generally contain higher profundal sediment pigment concentrations than do less productive lakes. The data obtained in this study supports this relationship. A nearly significant correlation ($r = 0.65$) was obtained between mean summer Secchi transparency and profundal sediment chlorophyll concentration. Secchi transparency has been shown to be a useful means of estimating the trophic status of lakes (Lasenby 1975, Carlson 1978).

High light, temperature and oxygen conditions have an adverse effect on pigment preservation (Vallentyne 1955). Therefore, differences between lakes with respect to their pigment concentration in the sediments may reflect either differences in productivity levels and hence the source of the pigments (allochthonous-autochthonous) or variations in pigment preservation.

In this study, the profundal sediment chlorophyll concentration did not statistically differ between meromictic and holomictic lakes. However, of the four meromictic lakes studied, only McGinnis Lake possessed a sediment chlorophyll concentration which was lower than the holomictic lakes. Therefore, it is believed that sample size has had an important contribution to the lack of significant difference between the two lake types with respect to their chlorophyll concentration. In contrast, the carotenoid concentrations in meromictic lakes were significantly higher than those in holomictic lakes.

A major difference between meromictic and holomictic lakes is the presence of an anaerobic monimolimnion in all meromictic lakes. The lack of oxygen in the profundal waters of meromictic lakes is thought by numerous researchers (Vallentyne 1955, Wetzel 1970) to enhance pigment preservation there. This fact is supported by my observation that the littoral to profundal ratio for carotenoid pigments was significantly greater in meromictic lakes than in holomictic lakes. Therefore, relative to the littoral pigment content of the sediments, meromictic lakes contained more profundal pigments than holomictic lakes. The increased profundal pigment concentration in meromictic lakes was undoubtedly influenced by their enhanced preservation in the anaerobic sediments of meromictic lakes.

It may be argued, however, that the source of the pigments differs between the two lake types. If it is assumed that the chlorophyll to carotenoid ratio is a reliable indicator of the relative allochthonous to autochthonous input (Gorham and Sanger 1972), then the chlorophyll to carotenoid ratios in this study indicated that in both lake types the source of the pigments was similar. Therefore, it is suggested that the difference in profundal pigment concentration in meromictic lakes in this study was a consequence of their better preservation in the monimolimnetic sediments of meromictic lakes.

4. Summary

The profundal sediments of meromictic and holomictic lakes statistically differed ($p < 0.05$) with respect to their iron and carotenoid contents. Based on comparative differences between littoral and profundal sediments, these differences appear to be influenced by meromixis. However, these results undoubtedly have been influenced somewhat by differences in sediment texture and age between zones of a lake. This is especially true for meromictic lakes whose littoral sediments contain large quantities of carbonates relative to that present in their profundal sediments. It is impossible with the available data to determine to what extent the carbonates have influenced the results.

C. The Surface Sediment Study in Retrospect

In this study, the interpretation of the data was somewhat speculative. The apparent or assigned cause for the observed differences may not, in fact, represent the ultimate causal factor. This, unfortunately, may reflect the manner in which the original problem was approached.

There are a number of ways that the surficial sediment study could have been improved. These improvements in turn may have provided more meaningful results. Unfortunately, given the limited time available, it was impossible to carry out a detailed survey of all ten lakes.

First, by homogenizing sediments along a particular transect, a great deal of information was lost. Variation along each transect was unknown and only an approximate variation was known within the lake based on differences between transects. Though it was assumed that the littoral values cited in the study were representative of the littoral sediments, it was not known how representative they actually were. It is suggested that a more intensive coring program of lakes with varying morphometry be undertaken in order to provide an estimate of the minimum number of samples required for good representation of the lakes' bottom deposits.

Secondly, by sampling the same depth of surface sediment (15 cm) in all lakes, sedimentation and hence age differences were ignored. It is quite conceivable that 200 years of accumulated sediments in one lake were compared to 50 years of sediment accumulation in another. It would be far better in a study of this nature, to locate the *Ambrosia* pollen horizon in each core and use this as a marker designating that depth for each core comparison.

Thirdly, the grouping of lakes as to their meromictic or holomictic status in some cases was based on a very limited number of observations. Lakes which were classified as holomictic may, in fact, be oligomictic and those which were classified as meromictic may also prove to be oligomictic as in the case of Sunfish Lake. Incorrectly classifying a lake will undoubtedly influence the results obtained. This problem is in part a result of our inability to clearly distinguish between meromictic and oligomictic lakes due to our inability to obtain sufficient long term data with respect to their circulation patterns upon which their definition is based (Loffler 1975). It is strongly suggested that those lakes which are believed to be meromictic should be monitored each winter to determine whether partial circulation ever occurs.

D. CRAWFORD LAKE CORE

The analysis of a sediment core from Crawford lake, a "known" meromictic lake, was undertaken with several objectives in mind. First, it was to be detemined whether any of the variables differed with respect to their stratigraphic pattern. The intention was not to be overly concerned with each temporal change that occurred, but more importantly, to determine whether similar temporal trends were exhibited between variables. Secondly, with respect to the observed trends, a possible causal mechanism was sought. Although a particular variable was expected to change due to the influence of other variables, it was particularly important to know whether some of these changes could be explained by the presence of development of an anaerobic monimolimnion.

According to Bortleson (1971), the primary factors controlling the abundance of organic carbon in sediments are:

1. the production of organic carbon within the lake,
2. the sedimentation of allochthonous organic matter,
3. the loss of organic material resulting from its chemical or biological degradation, and
4. variation in deposition rate of the whole sediment.

Work by Twenhofel *et al.* (1945) indicated that bacterial activity drops to very low levels in the sediments shortly after their burial. Thus, of the four factors affecting the abundance of organic carbon, point three is apparently the least important.

According to Mackereth (1966), the major source of sediment is that from a lake's drainage basin rather than from material produced within the lake. He states that "one may then regard the sedimentary sequence of a lake deposit as a series of samples of soils eroded from the drainage basin and deposited chronologically in the lake bed". Consequently, the composition of the sediment cannot be accounted for in terms of changing rates of organic productivity either on the drainage basin or within the lake itself.

In Mackereth's study, however, the mineral content of the sediments was rarely less than 60% whereas in Crawford Lake it was rarely above 55%. Therefore, in Crawford Lake, organic production within the lake and watershed may have played a far more important role in the temporal development of the profundal sediments than in Mackereth's study.

Changes in the organic matter content of the sediments may affect corresponding changes either directly or indirectly in each of the variables studied. Photosynthetic pigments because of their organic origin, would be expected to vary as the input of plant organic matter varies. Furthermore, the relative amounts of chlorophyll and carotenoids should differ in response to the relative contribution of allochthonous and autochthonous sources of organic matter (Gorham and Sanger 1972).

In the benthic community, chironomids utilize organic matter as a food source. Hence, in theory, with increasing quantities of organic matter, a larger chironomid community may be supported. This, in turn, will result in larger number of their remains being preserved in the sediments. It has previously been documented that a close correlation exists between the number of fossil chironomid remains and their species composition in recent sediments, with the living community (Iovino 1975). Thus, temporal changes in organic matter will result in temporal changes in chironomid remains, assuming however that no other factors (e.g., predation or parasites etc.) have an appreciable effect on the population.

Lastly, the iron and manganese input to a lake may be either enhanced or diluted in the sediment record depending on what fraction of the sediment they are bound to. According to Mackereth (1966), iron and manganese will be influenced more by conditions within the lake because they are easily affected by oxidation-reduction potentials. Pigments, however, as postulated in the literature, may be influenced by oxidation-reduction conditions through increased preservation if they enter an anaerobic environment. Through analysis of the core, it will be determined whether changes due to changes in productivity can be differentiated from changes due to increased pigment preservation. Lastly, with increases in organic matter, a larger littoral chironomid community may be supported. If an anaerobic profundal zone exists, then the organisms' distribution will be restricted to areas outside this region. However, temporal changes in the total number of chironomids inhabiting the profundal sediment, based on changes in a profundal core, will be difficult to determine if extensive slumping or secondary redeposition from the littoral zone occurs.

1. Sediment Chemistry

(a) Organic Matter and Carbonate Concentrations

Temporal changes in organic matter, carbonate and mineral content of the sediments are quite different in the sediments of Crawford Lake. At the bottom of the core the mineral content of the sediment was high (>70%), while both organic matter (<10%) and carbonate (<20%) were relatively low (Fig. 6). This is believed to be largely due to the poor soil development and lack of vegetation that existed within the watershed after glaciation. Numerous studies (Janssen 1968, Dodson 1977) have indicated a lack of tree pollen in the sediments during the initial stage of a lake's development. As terrestrial vegetation develops, the mineral content of the sediments is gradually diluted by increasing quantities of organic matter as a consequence of watershed stabilization.

In the top 200 cm of the sediment core, there occurs a distinct increase in organic matter and a corresponding decrease in the carbonate content when compared with that part of the core below 200 cm. During this same period, the mineral content of the sediment remains relatively unchanged, decreasing only slightly (Fig. 6). Adams and Duthie (1976) have shown for Sunfish Lake, a small calcareous lake, that a decrease in the relative carbonate content of the sediments was in part due to an increase in inorganic sedimentation. This inorganic sedimentation does not include carbonate precipitation. This phenomenon was not evident in Crawford Lake, primarily for two reasons. First, the mineral content of the core declined in relative abundance during the same period when carbonates underwent their largest decrease in concentration. Secondly, the relative abundance of the carbonate to the mineral content of the sediment differed between the top and the bottom layers of the core. The mineral content decreased by 25%, while the carbonate content decreased by only 1% between the top and bottom of the core. It seems more probable that the relative decline in carbonates was a consequence of increased production of organic matter.

(b) Iron and Manganese

Many factors influence the quantity of iron and manganese in the sediment of a lake (Mackereth 1966, Boyum 1976). The most notable of these are erosion intensity, migration of iron and manganese as influenced by redox conditions both within the watershed and the lake itself, and the rate of accumulation of the sediment (Adams and Duthie 1976). Given these factors, the interpretation of changing redox conditions within the lake must be carefully based on temporal changes in both iron and manganese and their ratio.

The iron and manganese stratigraphy in Crawford Lake was similar to that exhibited by the mineral content of the sediments. This was in marked contrast to both pigments and chironomid headcapsules which more closely resembled the organic matter stratigraphy.

Kjensmo (1968a) noted that the abundance of iron in the sediments of Lake Svinsjoen was closely related to the mineral content of the core from the same lake. The only depths where iron deviated from this relationship was in the top 45 cm. During this period, which according to Kjensmo, represented the meromictic phase of Lake Svinsjoen, iron increased in concentration (approximately 20 to 60 mg/g dry weight), as did the weight ratio of iron to manganese (5 to 35), while the mineral fraction decreased. In Crawford Lake, except for the deepest layer of bottom deposits, a distinct change in either the iron concentration or iron to manganese ratio such as that observed by Kjensmo was never observed. The high Fe:Mn ratio in the bottom deposits of Crawford Lake was typical of most lakes (Boyum 1976).

Throughout most of the Crawford Lake core, iron maintained a visibly close association with the mineral content of the sediments. Manganese, on the other hand (between 415 and 275 cm) exhibited greater variability with respect to both the degree and direction of its change relative to iron (Fig. 5). This may be due, in part, to the fact that manganese was more highly correlated with organic matter than was iron, thus reflecting changes in organic matter.

In the upper 275 cm of the core, the iron and manganese concentrations exhibited similar trends. The profiles of both were similar to that of the mineral content, suggesting a purely erosional mode of transport. This is in marked contrast to the lower portion of the core. In theory, since iron is associated with the mineral content of the sediment, a decrease in iron may occur as a consequence of decreased erosion. During the same period, the manganese concentration may increase if it is preferentially removed from the soils of the drainage system and subsequently deposited in the sediments. In order for this to occur, however, an aerobic profundal zone must be present, otherwise, manganese would go into solution and the manganese content of the sediment would decrease. In Crawford Lake, the manganese stratigraphy exhibited a general trend during which it decreased throughout most of the lake's history, suggesting the presence of an anaerobic hypolimnion. If Crawford Lake was meromictic throughout this period, then besides a decrease in manganese, an increase in iron (and in the iron to manganese ratio) ought to have been observed. This, however, was not found to be the case. Both iron and manganese exhibited decreasing trends while the iron to manganese ratio remained relatively constant (Fig. 9).

Kjensmo (1968b) attributed the increase in iron to the reprecipitation of iron as ferric sulphide. This may not have occurred in Crawford Lake to the same extent as it did in Lake Svinsjoen assuming

1. iron was present in the profundal waters, but in much lower concentrations or

2. redox conditions were unsuitable for the precipitation of ferric sulphide.

With respect to the former point, the iron in the profundal sediments of Lake Svinsjoen was ten times more concentrated than in the profundal sediments of Crawford Lake. It is of interest that in the profundal waters of some holomictic Finnish lakes, iron reaches sufficient concentrations to render them meromictic (Kjensmo 1962).

2. Fossil Chironomid Remains

In theory, the onset of meromixis should coincide with the permanent elimination of dissolved oxygen from the mud-water interface below the chemocline. This, in turn, should result in a concommitant decline in fossil chironomid remains in these profundal sediments. In this respect, Dickman *et al.* (1975) speculated that Pinks Lake had been meromictic since shortly after its inception because the number of fossil chironomid remains in its earliest profundal sediments (26/g dry weight) fell to a very low level (less than 10/g dry weight), shortly after its inception. In their study, the number of chironomid headcapsules present in the profundal core never exceeded 26/g dry weight.

In Crawford Lake, no permanent decline in the number of headcapsules was found (Fig. 7). They never exceeded 24/g dry weight and approximately 47% of the levels analyzed contained less than 5 headcapsules per g dry weight of sediment. However, in Crawford Lake, the number of headcapsules steadily increased in the surface 300 cm as did the percent organic matter. In contrast, Pinks Lake remained relatively constant with the exception of a peak during the hemlock pollen minimum and another earlier peak shortly after deglaciation. Given the stratigraphic pattern of chironomid remains in the Crawford Lake core, it would appear that the lake has remained meromictic since its inception and that extensive redeposition of littoral chironomid headcapsules has occurred.

Roback (1970) identified decreases in the total number of chironomid remains as a consequence of decreased organic matter and a drop in lake level. In his study, at the beginning of pollen zone C the lake level rose as a result of increased runoff into the lake which augmented the organic matter content entering the lake. Associated with the large increase in organic matter was a sharp increase in the number of chironomid remains in the profundal core. Furthermore, the remains were largely comprised of littoral zone species. In Crawford Lake, it would appear that the gradual increase in organic matter was also accompanied by a gradual increase in fossil chironomid headcapsules. It is quite conceivable that chironomids living above the chemocline are re-distributed when partial circulation of the upper water layers occurs. Thus, some of these would be deposited in the monimolimnetic sediments. Lastein (1976) has shown that during fall circulation, extensive resuspension of the profundal sediments occurs. If this does occur, however, it will be influenced somewhat by lake morphometry, climate and the distribution of the chironomid community. In Crawford Lake, the resuspension of littoral chironomid headcapsules and organic matter appears to have been limited by its basin morphometry which prevents most of the winds from reaching its surface waters.

It is suggested that the observed increase in the organic matter content of the littoral sediments of Crawford Lake (300-0 cm) has resulted in increased food availability for the benthic organisms. This, in turn, would be reflected in the maintenance of a larger littoral chironomid population. Due, however, to the limited amount of redeposition that occurs, only a small percentage of the chironomid headcapsules are deposited in the profundal sediments. It is of interest in this respect to note that the fossil diatom remains from the Crawford Lake profundal surface sediments were primarily resuspended littoral zone species, with relatively few planktonic species present (J. Smol, per. comm.). Therefore, although chironomids may not inhabit permanently anaerobic profundal sediments, their redeposition there makes them suitable as a paleolimnological indicator of meromixis only when the rate of littoral sediment resuspension and slumping can be independently assessed. For this reason, the ratio of profundal to littoral zone chironomid indicator species should be determined in each sediment sample.

3. Pigments

During its development, Crawford Lake underwent substantial changes in productivity as reflected by changes in fossil pigments. The top 200 cm of the core represents a much more productive period of the lake's history than the lower portion of the core. Numerous authors (Vallentyne 1954, Czcuga *et al.* 1966, Wetzel 1970, Adams *et al.* 1976) have also found that lakes are generally unproductive immediately after glaciation, but then exhibit an increase in productivity levels as evidenced by fossil pigments. Throughout the post-glacial period, these lake sediments appear to fluctuate in fossil pigment concentrations indicating that lake productivity was not constant but varied with climate, soil and vegetation type.

In Crawford Lake sediments, the chlorophyll and carotenoid pigment decomposition products in the sediments exhibited changes which were similar to changes in the concentration of organic matter ($r = 0.872$ (chlorophyll) and 0.910 (carotenoids)). Changes in fossil pigment concentration as a result of increased preservation were never identified. The only significant changes that were observed could be accounted for by increased inputs of organic matter. There, it would appear that Crawford Lake has sustained an anaerobic hypolimnion throughout all but its earliest history.

4. Summary

The relatively minor changes that have occurred in the iron and manganese concentrations and their ratio, in contrast to changes observed by Kjensmo (1968) and Boyum (1976) suggest that relatively stable conditions have existed throughout most of Crawford Lake's history, with respect to reducing conditions in its hypolimnetic waters.

Fossil chironomid headcapsule remains were relatively low throughout the lake's development. Temporal variations in chironomid remains coincided with changes in organic matter, suggesting that redeposition from the littoral to profundal zone occurred. Presumably, the number of remains redeposited was relative to the number present in the littoral sediment. Therefore, it is suggested that Crawford Lake has been meromictic since shortly after its inception.

Conclusion

In conclusion, the surface sediment study suggested that both iron and carotenoids were significantly higher in the profundal sediments of meromictic lakes than in the profundal sediments of my holomictic lakes. This conclusion was based on a comparison of littoral to profundal iron and carotenoid ratios in 4 meromictic and 6 holomictic lakes. However, it was not possible, with the available data, to show conclusively that this was a result of meromixis. A more detailed analysis of each lake would be required in order to evaluate how representative the littoral and profundal concentrations are for each variable. In a number of instances (i.e., profundal Fe:Mn ratio and chironomid headcapsule densities) though, no statistical differences were present (at the 95% confidence level), the data was highly suggestive (i.e., significant at the 90% confidence level). This was believed to have been influenced somewhat by sample size.

The Crawford Lake profundal core demonstrated that temporal changes in most variables studied were closely correlated with variations in either organic matter or mineral content of the sediments. During its development there was no indication of a transition from holomictic to meromictic status. Therefore, given the morphometry of Crawford Lake and its well-protected basin, it is believed that it has been meromictic since shortly after its inception.

In this study, the variables iron and manganese appear to be the most useful paleo-indicators of meromixis. This is largely due to the speed and accuracy with which both may be determined and their different behaviour under reducing and oxidizing conditions.

Total fossil chironomid headcapsule remains are not a suitable paleoindicator since they are subjected to secondary redeposition. However, it is strongly believed that if they are identified as to littoral or profundal species that they would then represent a far more useful indicator of meromixis in paleolimnological studies. The largest drawback to their use is the relatively low density in which they are present and hence the large amount of sediment required in order to obtain statistically reliable numbers.

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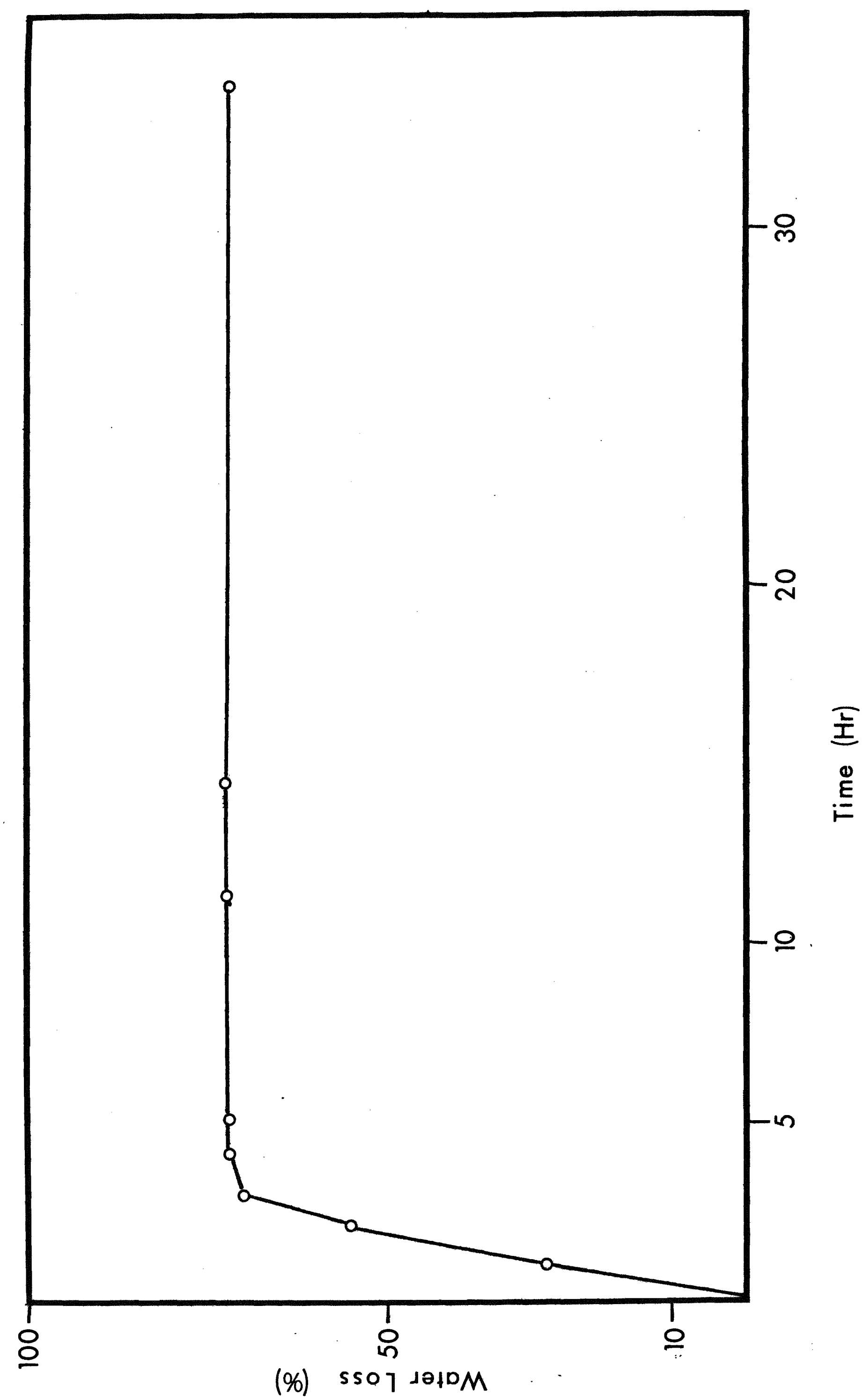
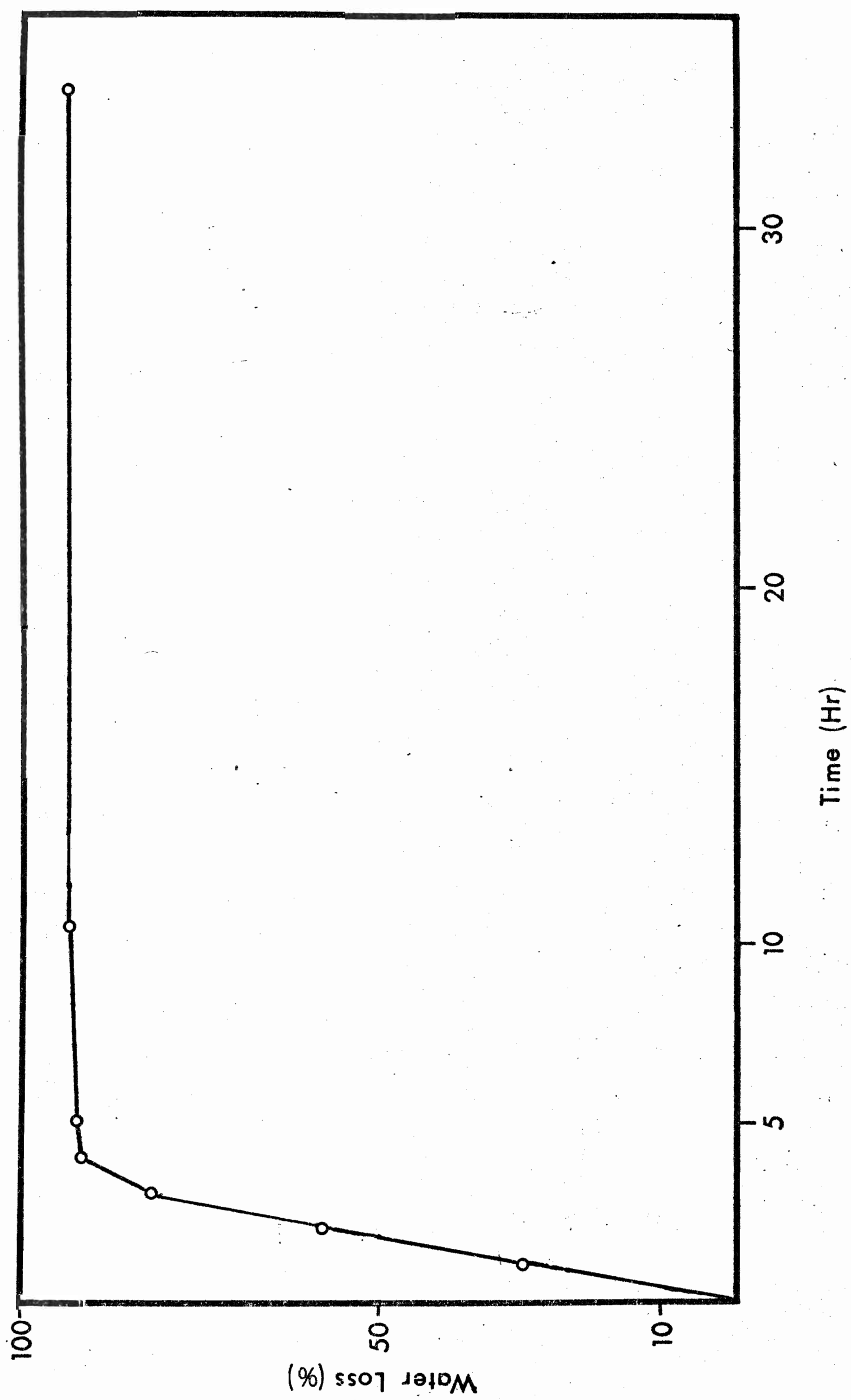
Appendix A

Figure 17. Temporal water loss (%) from surface sediment at 95°C



Water Loss (%)
100
50
10
Time (Hr)
5
10
20
30

Figure 18. Temporal water loss (%) from surface sediment at 95°C



Water Loss (%)
100
50
10
Time (Hr)
5
10
20
30

Appendix B. Source of morphometric maps used in this study

Lake	Source
Little Round	McNeeley (1973)
Pinks	Dr. M. D. Dickman, Department of Biological Sciences, Brock University
Crawford	Boyko (1973)
McGinnis	Dr. R. Jones, Department of Biology, Trent University
St. George-1, 2	Charlton, S. (1977).
Coon	Dr. D. Lasenby, Department of Biology, Trent University

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Addendum UNDERESTIMATION OF FOSSIL CHLOROPHYLL CONCENTRATIONS IN MEROMICTIC LAKE SEDIMENTS THROUGH THE USE OF A CORRECTION FACTOR

It has been suggested that the use of a correction factor for background absorbance at 750 nm may yield a "gross" underestimation of pigment concentrations in meromictic lake sediments. This underestimation, if it occurs, would reflect the absorbance, at 750 nm by fossil bacterial photosynthetic pigments (Brown, per. comm.). In order for this to occur meromictic lakes must contain first a significantly larger photosynthetic bacterial population than holomictic lakes and secondly the fossil bacterial chlorophylls present in the sediments must exhibit a maximum absorbance at 750 nm.

It is generally accepted with respect to the first point, that meromictic lakes contain a larger photosynthetic bacterial population than holomictic lakes. This reflects the presence of a permanently anaerobic monimolimnion which is high in hydrogen sulphide. The photosynthetic bacteria utilize hydrogen sulfide as a hydrogen ion donor during photosynthesis rather than water as occurs in plants. Therefore, in the sediment record, (assuming bacterial pigments exhibit a maximum absorbance at 750 nm) meromictic lake sediments should have a significantly larger correction factor than do holomictic lakes as a consequence of their greater photosynthetic bacterial populations. The problem however, is further complicated as different species of photosynthetic bacteria exhibit a maximum absorbance at different wavelengths when extracted in acetone, none of which are 750 nm (S. Severn, per. comm.). Therefore, if fossil bacterial chlorophylls are present in sediments they may not be detected by measuring light absorbance at 750 nm. Furthermore, to the best of my knowledge, no one to date has conclusively shown that in the sediments fossil bacterial chlorophylls do in fact absorb maximally at 750 nm.

The above problem was examined in order to assess whether the background absorbance at 750 nm was significantly greater in meromictic lake sediments than in holomictic lakes.

Table 21 shows the absorbance at 750 nm expressed as a percentage of the absorbance at 667 nm (chlorophyll SPSU). The Mann Whitney-U test was applied in order to estimate whether the correction factor used in the meromictic lake sediments significantly differed from those in holomictic lakes. All littoral sediment transact values were averaged per lake (see methods).

In all instances (littoral, profundal and littoral to profundal ratio comparison) meromictic lakes did not significantly differ from holomictic lakes. Therefore if bacterial fossil pigments were present in the sediments they did not significantly contribute to the correction factor of meromictic lakes. Hence in this study it is believed that fossil chlorophyll SPDU's were not underestimated in the meromictic lakes studied.

Table 21. Absorbance of acetone extracted sediment at 750 nm expressed as a percentage of the absorbance at 677nm in the surface sediments of selected meromictic and Holomictic Lakes

Lake	littoral (%)	Profundal (%)	L/P
Crawford	4.69	1.0	4.69
McGinnis	11.16	40.3	0.28
Pink	4.07	9.7	0.42
Little Round	5.33	12.0	0.44
St. George$_1$	5.21	7.9	0.66
St. George$_2$	4.65	11.35	0.41
Coon	6.37	4.15	1.53
Found	1.48	3.4	0.44
White Duck	1.50	1.45	1.03
Canoe	5.38	4.07	1.32
U	9	7	8.5
Significance	NS	NS	NS

ADDENDUM B SEDIMENT DISTURBANCES AND ITS EFFECT ON DATA INTERPRETATION

In the analysis of sediment cores it is assumed than no major disturbances have occurred in the profundal zone so as to alter the seasonal deposition of sediments. Transport by water turbulence and slumping caused by the angle of repose are ignored. If they do occur during a lakes' development, then erroneous conclusions may be made, based on the sediment record. For example, it is known that sedimentation rates differ between lakes and hence the surface 20 cm of sediment may represent differing temporal sinks for fossil accumulation comparisons between lakes. If slumping were to occur in some of the lakes studied, then this would effectively exagerate the size of the temporal sink in, between lake comparisons. Consequently, potential differences between meromictic and holomictic lakes could theoretically reflect differences in sedimentation rates as a function of slumping rather than a function of the physical state that differentiates the two lake types. In contrast, the lack of significant differences between the two lake types with respect to their sedimentary fossil record, may reflect the effect of slumping, thus destroying any differences between the two lake types, induced by meromixis.

Lakes, in which the entire core exhibits annual varves, disturbances such as slumping can be readily recognized due to either a disruption of the varves, or sudden increases in the apparent sedimentation rates (i.e. distance between varves). In non-varved cores, the problem is less readily recognized.

Davis (1968,1973) has shown that sediment deposited in the littoral zone eventually make their way to the profundal zone through a process of resuspension. Furthermore the accumulation rate of sediment in the produndal zone is in turn influenced by basin morphometry (Lehman 1975). Presumably in such a process a selection for more organic material occurs with heavier slits remaining in the littoral zone. In this study the profundal sediments of all lakes contained greater quantities of organic matter than did their respective littoral sediments. Therefore, should slumping of littoral sediments occur during a lake's development, both a decrease in organic matter and an increase in the mineral content of the sediment should be evident.

If sediment accumulates midway down a lake's basin, there may be very little difference in the physical characteristics of these sediments than those found in the profundal sediments. Therefore, unless there is some marker or line that indicates what angle material is deposited it may be very difficult to assess whether slumping has occurred without assessing the age of each sediment strata.

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ADDENDUM C

SOLUBILITY PRODUCTS

Redox potential

In this study it was assumed than changing oxygen concentration and its effect on the redox potential, was the only factor influencing the direction of movement of both iron and manganese across the mud water interface and in turn the solubility products formed. It is known however that pH, CO_2, Sulphur and carbonate concentrations will also influence the solubility products present within any aqueous solution (Garrels and Christ 1965). Therefore in this study, dividing the lakes into two groups (meromictic and holomictic) on the basis of one characteristic (oxygen) may have obscured the influence such variables as pH, CO_2, sulfur, and carbonate concentrations had on the iron and manganese content of the sediments.

The pH is generally considered the most important variable with respect to its influence on the redox potential and in turn the stability of various minerals that form in response to changing redox conditions (Degens 1965). A rise of pH of one unit is accompanied by a fall in redox potential of 58 mv. Therefore redox potentials are often corrected to pH 7 by subtracting 58 mv for every pH unit on the alkali side of neutrality, and by adding 58 mv for every pH unit on the acid side of neutrality. Generally the surface waters of most north temperate lakes lie between pH 6 and pH 8 (Hutchinson 1957) and rarely differ by more than 2 pH units from top to bottom (Wetzel 1975). Therefore the change in redox potential as a consequence of changing pH is relatively small.

In fully oxygenated surface water redox potentials lie between 300 and 500 mv. In neutral fully oxygenated water which is in equilibrium with air, redox potentials slightly greater that 500 mv are obtained. The redox potential remain relatively constant down to about 2 ppm of oxygen. Therefoere in most holomictic lakes whose water column is well oxygenated, pH will have a greater influence on the redox conditions. However, as the oxygen concentration of the water approaches zero parts per million, as in the monimolimnion of meromictic lakes and the hypolimnion of some eutrophic lakes, the redox potential will decrease below 100 mv. This latter change in redox potential as a function of changing oxygen concentrations is much greater that would occur due to changing pH. Therefore, in this study distinctly different oxygen stratigraphies differentiating meromictic from holomictic lakes would have had a greater effect on the redox potential than pH.

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ADDENDUM D PIGMENTS

1. <u>Epiphasic-Hypophasic Carotenoids</u>

Two basic types of carotenoids (carotenes and xanthophylls) occur in plants. The carotenes or epiphasic carotenoids consist exclusively of carbon and hydrogen while the xanthophylls or hypophasic carotenoids, contain carbon, hydrogen and oxygen (Devlin 1969).

In both the water column and the sediment of lakes, a preferential destruction of xanthophylls occurs. This may be attributed to the greater susceptibility to attack of xanthophylls by molecular oxygen. Therefore, one would expect a higher epiphasic to hypophasic carotenoid ratio (carotenes: xanthophyll ratio) in holomictic lake sediments relative to those in the sediment of meromictic lakes. This would reflect the longer time period that holomictic profundal sediments are subjected to oxygen relative to sediment from the monimolimnion of meromictic lakes. Therefore, the epiphasic to hypophasic carotenoids ratio represents another potentially useful paleolimnological tool for differentiating between meromictic and holomictic periods during a lakes ontogeny.

2. <u>Cis-Trans Isomers</u>

Vallentyne (1965) suggested that cis-trans isomerization of carotenoids might occur in lake sediments, thus leading to the formation of carotenoids not originally present in the deposit. Since cis-trans isomers exhibit an absorbance maximum at lower wavelengths than the all-trans form it is possible that the cis-form was not estimated in this study, hence underestimating the total carotenoids concentration. The trans-form

B-Carotene, when extracted in hexane exhibited a peak absorbance at 451 nm, as compared to 447 and 444 nm for its cis-form, Neo-B-Carotene-U and Neo-B Carotene B respectively (Vallentyne 1957).

The full impact on this study of not having measured the cis-isomers hence underestimating the total carotenoid concentration, will depend upon a number of factors. First, it is important to know what percentage of naturally occurring carotenoids are cis-isomers. If for example, they represent a large proportion of the total carotenoids then the total carotenoid concentration may have been severly underestimated. However, if they comprise only a small portion of the total carotenoids then not having measured them may not have significantly influenced my results. Secondly, when the pigments have been deposited in the sediments it is useful to know whether isomerization occurs. This will provide some insight as to whether or not similar cis-trans ratio found in living plants should be expected in the sediments. Lastly, when extracting pigments from the sediments it is important to know whether isomerization can be induced.

The major portion of the naturally occuring carotenoid molecules and the most stable have all their double bonds in the trans configuration (Conn and Stumpf 1972; Weedon 1965). Goodwin (1965) however acknowledgeds the fact that traces of cis-isomers probably exist in leaves but claims that their occurrence must always be considered critically because isomerization can take place artificially during extraction.

Therefore, since naturally occurring cis-isomers represent such a small proportion of the total carotenoids, I believe that they would not have significantly influenced the results obtained in this study.

If isomerization from the trans to cis form occurs in the sediments, then because the trans form comprises the largest proportion of carotenoids, they may in fact have been underestimated.

In sediments there is a distinct lack of cis-isomers (Vallentyne 1960). He belived that something in the sediments either hinders steric transformations or else shifts the equilibrium position in favour of the all-trans form.

Stereomutation of carotenoids occur under a variety of conditions. In extracting carotenoids, oxidation and cis-trans isomerization may occur if carotenoids in solution are left in the light, in warm conditions, or in the presence of air. All carotenoids undergo cis-trans isomerization on irradiation in solution, with light of wave-lengths corresponding to the main absorption band being most effective. Furthermore steromutation of a carotenoid begins immediately on solution. The process is usually slow at room temperature and more rapid at elevated temperature. However according to Weedon(1965) in benzene and a light-petroleum solution in diffuse daylight only 1-2% of carotene undergo steromutation in 24 hours. Therefore, given the lack of naturally occuring cis-isomers, their absence in sediments, and the relatively low stereomutation that occurs during extraction, it seems unlikely that the total carotenoid content of the sediments in this study were under-estimated.

Effect of Grazing

In this thesis, it was stated that the three most important factors resulting in increased pigment degradation were:

1) high light intensities
2) high temperature
and 3) high oxygen conditions.

Since light and temperature conditions are similar in meromictic and holomictic lake, it was believed that the presence of a permanently anaerobic monimolimnion in the former, would result in enhanced pigment preservation in the profundal sediments of meromictic lakes. However, Daley and Brown (1973) indicated that chlorophyll diagenesis takes place primarily, if not exclusively, by photochemical oxidation following cell lysis. Therefore, further degradation which occurs in the sediments may be very small relative to that which occurs as the pigments pass through the water column. If this is so then it is questionable whether the differences in sediment pigment concentrations between the two lake types found in this study can be attributed solely to meromixis.

A fourth factor (grazing by herbivores) not discussed in the thesis has been shown to substantially increase pigment degradation (Daley 1973). In Daley's experiments in which *Daphnia pulex* were allowed to feed on *Anacystis nidulans* and *Scenedesmum quadricauda*, the exact mechanism by which the herbivores destroyed the chlorophyll molecule was not known, although it was believed to be enzymic in nature (Daley 1973). In contrast Porter (1975) indicated that algae with durable cell walls, gelatinous sheaths or masses of colonial cells can pass through the gut intact in some grazer species and remain viable. Therefore the total impact of grazing on the sediment pigment concentrations will depend upon both the susceptability of each phytoplankton species to cellular lysis in passing through the zoplankton gut and their relative pigment contribution to the sediment record. Furthermore, the ultimate effect herbivore grazing has on sediment pigment concentrations will depend upon those factors that in turn influence zooplankton grazing. Wetzel (1975) has indicated that each of the following are important factors influencing zooplankton filtration and feeding rates:

1) food particle size
2) concentration of food particles
3) body size of zooplankton
4) water temperature
5) oxygen concentrations.

Consequently differences in the sediment pigment concentration that occurred between the two lake types in this study may simply reflect the grazing effects of zooplankton. However, the full impact that this may have on pigment degradation has yet to be substantiated.

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